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THE FUNCTIONAL AND COMPARATIVE ANATOMY OF ITS
MUSCULAR AND OSSEOUS SYSTEMS.

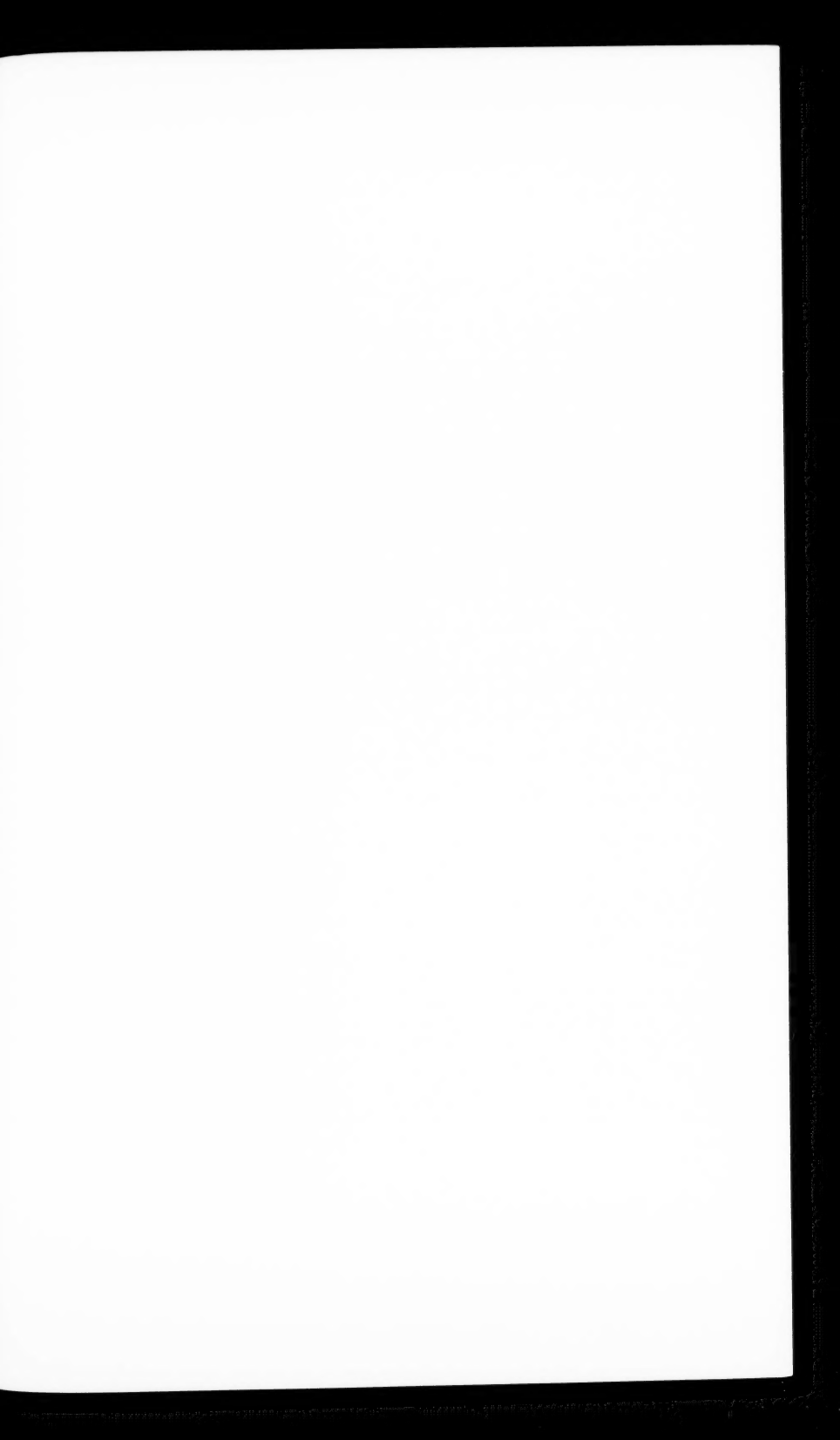
By A. BRAZIER HOWELL.

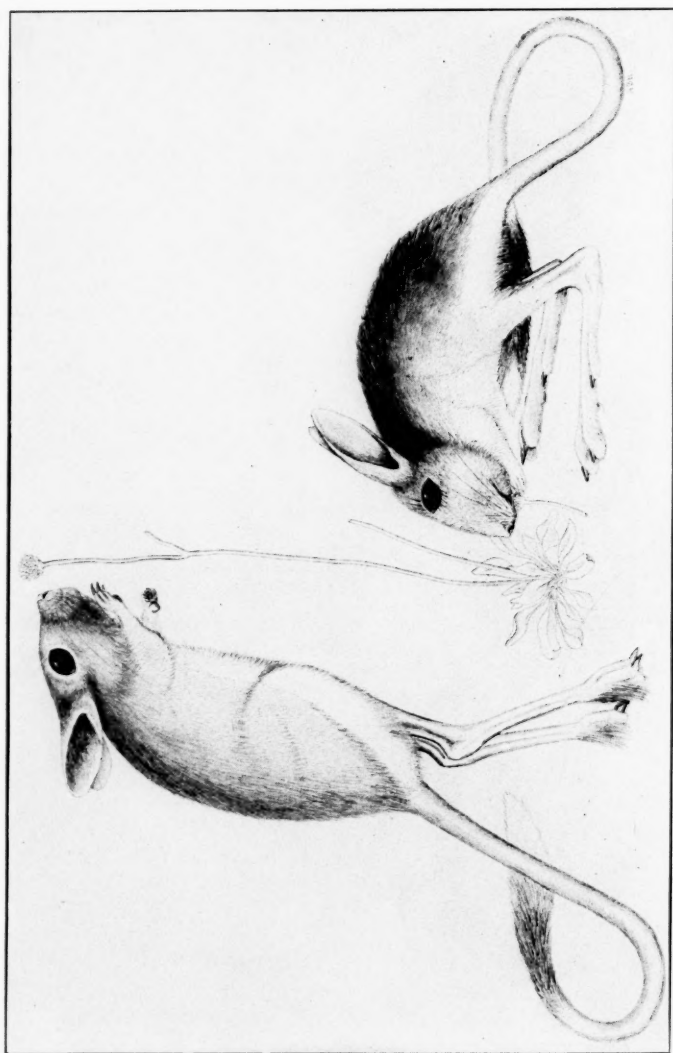
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(Continued from page 3 of cover.)

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FRONTISPIECE. The Egyptian jerboa (*Scirtopoda*, left) and the Chinese five-toed jerboa (*Allactaga*, right).

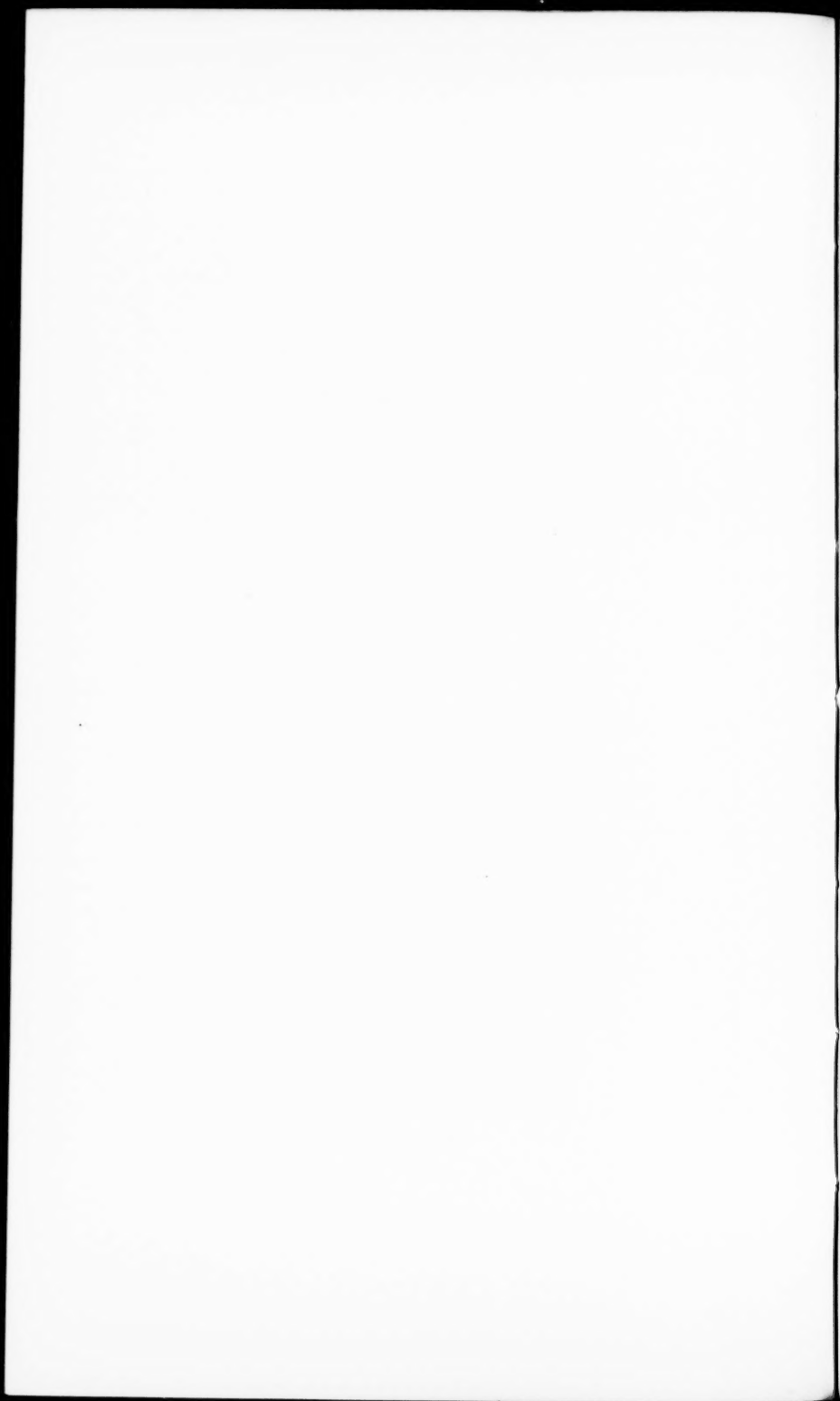
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INTRODUCTION.

As an important detail in the program of the writer to investigate and report upon the morphology of diverse groups of mammals especially adapted for particular modes of progression, work upon saltatorial and fossorial rodents was started some ten years ago. After making considerable progress these projects were laid aside until a greater variety of material could be secured. Many rodents of diverse affinities, in many parts of the world, have become independently adapted in high degree for progression by saltation, and it was desired especially to obtain for study such forms as the 4-toed jerboa (*Scarturus*) and the Australian jerboa mice *Notomys* and *Ascoppharynx*, the last with its peculiar external gular pouch. After a number of years, however, this desire seems no nearer realization, and rather than delay the project indefinitely it was determined to offer the present contribution as a study of the anatomy of one of the most interesting of New World rodents, the kangaroo rat *Dipodomys*, in comparison with such forms of the Old World jerboas as could be secured. For the reason that comprehensive reports of the myology and osteology of the more interesting of our small mammals are so seldom undertaken, the present work is offered in considerable detail, with especial reference to the saltation features and the convergence exhibited by the two groups. Some of the myological details of the jumping mouse *Zapus* are also mentioned, and osteological ones of the large African saltator *Pedetes*, as well as comparison of external features of a number of other genera available. Only a partial, and rather meager, discussion of results is offered, however. The conclusions resulting from this study will be presented in a separate paper, discussing in detail the comparative saltatorial and cursorial modifications of marsupials, insectivores, primates, rodents, lagomorphs, and ungulates, with special reference to the basic principles involved.

In the accompanying drawings no uniform scale was employed. For such features as the shank and thigh, the different details appearing on a single plate were all drawn the same actual size so as to facilitate comparison.

MATERIAL.

With the exception of a single skeleton of *Scirtopoda* originally donated by me to the Museum of Vertebrate Zoology of the University of California several years ago and later borrowed, all the material upon which the present study was based is in the collections of the United States National Museum. In this connection I wish to express appreciation for the helpful coöperation of the U. S. Biological Survey, through the courtesy of Dr. E. W. Nelson and Dr. W. P. Taylor, in securing for my use numbers of spirit specimens and of skeletons of *Dipodomys spectabilis*, which is one of the largest (and hence most desirable for dissection) forms of this genus. I have had access to two spirit specimens, one complete skeleton, and numerous skins and skulls of the 5-toed, Asiatic jerboa (*Allactaga mongolica longior*), obtained some years ago by A. deC. Sowerby. Of the 3-toed, Egyptian jerboa (*Scirtopoda orientalis*), I have had one complete and one incomplete skeleton and two spirit specimens, the latter originally secured in the vicinity of Alexandria, Egypt, by the late John Hornung. I purchased these specimens years ago and later presented them to the National Museum. Of further specific interest are a skeleton of the African *Pedetes*, skins and skulls of the Asiatic 3-toed jerboa *Dipus sowerbyi*, the type skin and skull of the rare *Euchoreutes naso alashanicus*, and a dissected specimen of the genus *Zapus*. Specimens, including skeletons, of other genera and species of the Heteromyidae (pocket mice and kangaroo rats) have also been used to some extent, as well as of the wood rat *Neotoma*, various sorts of squirrels, and many miscellaneous mammals of more or less saltatorial habits.

In the following pages where *Dipodomys*, *Allactaga*, and *Scirtopoda* are mentioned without statement of the species, reference is to the forms dissected, as mentioned above.

AFFINITIES.

No historical résumé of the nomenclatural changes experienced by the animals discussed will here be offered, but a few words regarding relationships will be in order. The genus *Dipodomys*, constituting the chief subject of the present paper, belongs to the family

Heteromyidae. *Perodipus*, long recognized as a genus on the basis of its possession of a hallux, is considered to be a synonym, as suggested by Grinnell (1922), for the reason that in certain forms the hallux is present in some individuals and absent in others. *Dipodomys* is the most saltatorial genus of this family, but the little kangaroo mouse *Microdipodops* has more specialized cranial features.

Of more generalized form are the genera *Perognathus* (with subgenera *Perognathus* and *Chaetodipus*), *Heteromys* and *Liomys*, some features of which are herein discussed. This family, as pointed out more specifically by Miller and Gidley (1918), belongs to the superfamily Sciuroidea, and hence it is fitting that the features of *Dipodomys* should be compared with those of some of the squirrels of the family Sciuridae, which has been done from time to time. Of interest in this connection also are some of the characters of the pocket gophers, of the family Geomyidae, belonging to this superfamily, for geomyids are the closest living relatives of heteromyids, and the two groups agree in being the only living mammals with capacious, bilaterally symmetrical, external cheek pouches.

Comparisons have frequently been made in the following pages with features of the wood rat *Neotoma* simply for the reason that a study of this animal, as representing a fairly generalized rodent, has previously been made. Actually, however, its relationship to the kangaroo rat is rather distant, for *Neotoma* belongs to the family Cricetidae (or Sigmodontidae if one prefer to consider the New World members as constituting a separate family) of the superfamily Muridae.

To the superfamily Dipodoidae belongs the family Dipodidae or jerboas. In this superfamily is also *Zapus*, of the family Zapodidae, and *Pedetes* of the family Pedetidae, both of which are herein mentioned. The jerboas that have been dissected in this connection are the 3-toed Egyptian animal long known as *Dipus aegyptius* but termed in later years *Scirtopoda orientalis*, and the 5-toed Asiatic jerboa of the form *Allactaga mongolica longior*. Proportions and skull characters of the 3-toed Asiatic species *Dipus sowerbyi* have also been given, but the comparative material is too scanty for me to have attempted to pass upon the generic status of this animal. The jerboa of the genus *Euchoreutes* is discussed elsewhere. A single poorly preserved specimen of this mammal has been examined, but none of the interesting 4-toed *Scarturus* from Africa, the remarkable little *Salpingotus* from northern Asia, or the genus *Cardiocranius* of China.

HABITS OF THE KANGAROO RAT.

In order that the bodily form and the functions of the different structures of a specialized mammal may be evaluated with some intelligence it is necessary that one consider its habits and habitat.

The genus *Dipodomys* is distributed over the open country of western North America from Montana to the Valley of Mexico, and from Kansas and Texas to the Pacific Ocean. On the whole it is found in open country but is not confined to this type of habitat. In prairie country it is at home in the short grass lands, often devoid of brush, but over most of its range there are at least scattered bushes of sage, greasewood, or other shrubs characteristic of an arid region; and the genus is often particularly well represented in some sections of California quite densely grown to chaparral. It seems highly probable, however, that the latter type of habitat has been secondarily invaded from contiguous areas of a more open character. Invariably, however, the preferences of the genus are for surroundings with arid tendencies. In parts of its range the genus is found where the winter rains may be relatively copious, and there may even be rather low summer temperatures accompanied by frequent fogs (as in the case of *D. m. goldmani*, near Monterey, Calif.), but always the immediate habitat is of an arid character, and individuals will never be found, in any part of the range of the genus, in low, swampy areas amid lush vegetation.

In the main, also, kangaroo rats will not be found in areas where the ground is covered by large rocks, nor are the animals partial to hard ground. There are exceptions to the latter rule and occasionally they occur where the ground is both hard and covered with small, loose rocks. But preference is very definitely shown for soil that is deep and loamy, and especially for the more sandy type of soil. One species (*D. deserti*) is practically confined to deposits of aeolean or drifting sands, and as these are usually very light in color, the paleness of the coat of this species may be considered to be correlated therewith.

When conditions chance to be favorable kangaroo rats may occur in great numbers so that dozens may be caught in the collector's traps during a single night. It is therefore indicated that in their normal range they are fully as successful a mammalian type as the ground squirrel, meadow mouse, and other rodents which are ecologically aggressive.

Most species of *Dipodomys* do not construct elaborate burrow

systems, possibly because of their weak digging equipment. Mostly the home consists of a rather short and shallow burrow with two entrances and a side chamber for a nest, or at times (possibly in the case of a vagrant male), a tunnel but little more than a foot long will be constructed. But in most cases there will be employed an added safety factor in the shape of a loose earthen plug, closing the entrance from the inside. It is probable that even when this is lacking at the entrance the sleeping chamber is so closed.

Some of the species which are more particular in their habitat preferences may be gathered by the exigencies of their surroundings into small colonies, or some sorts may actually be colonial to a slight extent. It seems that this may be the case with *D. deserti*, which often constructs series of galleries that are more elaborate than usual. This may be partly attributable to the fact that the burrows are usually in sand that is so loose that the tunnels collapse in part upon the slightest provocation, when a new gallery must be initiated.

Dipodomys spectabilis, the species upon which the present article has been based, most often occurs in a type of loam more clayey than sandy. Its habits are remarkable in that it constructs a "mound" of extensive tunnels. Where the animals occur these are dotted over the landscape, each mound "ranging from 6 inches to 4 feet in vertical height, and from 5 to 15 feet in diameter" (Vorhies and Taylor, 1922). They are occupied for years, the earth excavated being deposited about the entrances, thus raising the latter above their surroundings. Whether constructed with this purpose or not, the fact remains that this slight elevation serves to protect many of the burrows on flat ground from the flooding that they would otherwise experience during the occasional torrential rains of summer.

At first thought it is somewhat surprising that rodents having the weak fore feet of *Dipodomys* should construct fairly elaborate burrow systems in ground which at times is not at all soft. But weak tools are effective when wielded with proper industry, and the latter is undoubtedly an ingrained character, for the reason that proper underground retreats are certainly more necessary for the survival of this dweller of the open spaces than for most other rodent genera.

The characteristic digging posture is for the animal first to elevate its posterior quarters (as in fig. 3) and to scratch rapidly with the fore feet. This is followed by vigorous kicking with the hind feet, for the purpose of ejecting to the rear the earth loosened by the fore feet. The animal may then back for a short distance before repeating the latter action and in this manner the earth may be transported

throughout the length of a burrow. I have never observed any other method of moving earth, so I am unable to state how a burrow entrance is plugged from the inside. Some tamping action by the fore feet must be involved in this, however.

The species of kangaroo rat which inhabit the more elevated or rigorous part of the genus' range must either hibernate during the winter months or else remain torpid for considerable periods. In the colder parts of the range of *D. spectabilis*, as about Flagstaff, Arizona, it is likely that there are winter spells of suspended or at least greatly reduced activity lasting for many days at a time, but in the milder sections, as about Tucson, the only suspension of surface activity is experienced during periods of storms or unusual cold, lasting for not more than two or three days at a time. Nevertheless food is stored in the burrows more industriously than is perhaps the case with any other rodent of the region.

This habit of food storing is a deep-seated instinct and must be classed as one of the major behavioristic urges. Even an animal that was freshly removed from a trap, with an injury that must have caused considerable inconvenience, feverishly set to work without delay moving a pile of grain from a corner of its cage to better concealment at the opposite end. I have watched long and intently in an effort to learn the actions involved in the use of the external cheek pouches, but unsuccessfully. Food is rapidly passed, by means of the fore feet, into first one and then the other pouch. The fore feet also aid in rapidly emptying the pouches of their contents.

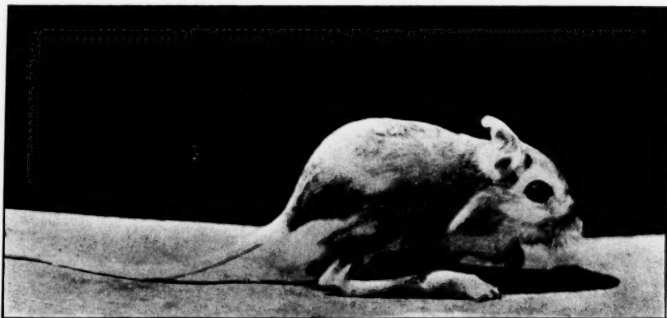
Vorhies and Taylor (1922) have demonstrated that this species of kangaroo rat is partial to a long list of plant foods, but the principal items consist of grass seeds and root stocks of grasses, which are transported in the cheek pouches and stored in side chambers of the burrows until needed during periods of food shortage. But little green food appears to be taken, even when available, although a variety of juicy roots is consumed. It is doubtful if the animals ever deliberately seek water, although some free water is probably taken into the system when this occurs in the form of dew, or vegetation has been wet with rain.

Certainly the ability of at least some species of the Heteromyidae to dispense with free water is most remarkable. It is true that in captivity many sorts will regularly drink considerable quantities of water if this be supplied, but the same species appears to thrive equally well without this item. Kangaroo rats have upon a number of occasions been kept in captivity for many months upon an ex-

clusive diet of dry grain and without water. I myself have kept a pocket mouse (*Perognathus*) for thirteen months in a cage situated in my garage. During this time it was fed dry rolled oats and nothing else, either liquid or solid.



Vernon Bailey photo.



A. deC. Sowerby photo. courtesy T. F. Unwin.

FIGURE 1. Convergence of form for saltation, as exhibited by the American kangaroo rat *Dipodomys spectabilis* (above), and the Chinese jerboa *Dipus sowerbyi* (below).

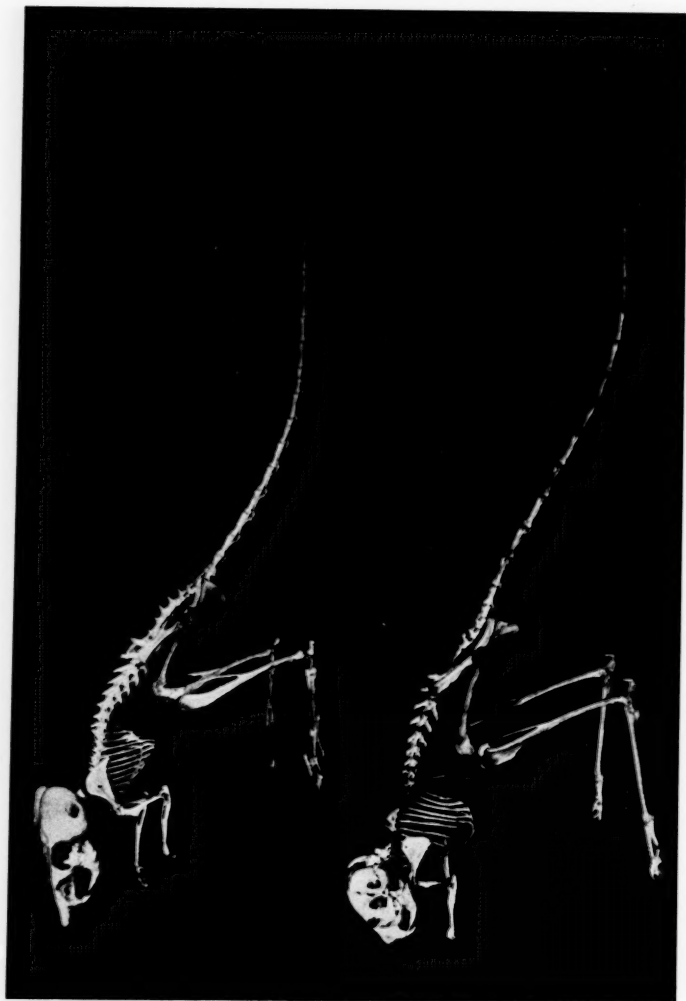


FIGURE 2. Mounted skeletons of kangaroo rat (*Dipodomys deserti*) and Egyptian jerboa (*Scirtopoda orientalis*).

It is well known, of course, that mammals derive sufficient moisture from the metabolism of their food for their physiologic needs save, in the majority of instances, those connected with excretion (Babcock, 1912). But it is extremely doubtful that such metabolic water can be manufactured in more copious amount by the desert dweller than by its relative of more humid clime. In other words it seems certain that the products of metabolism of a given rate are the same regardless of the mammal concerned, and the physiology of digestion, quite thoroughly known, will not admit of any process whereby either more or less than a definite quantity of water may be derived by the metabolism of a given quantity of any particular food substance. Therefore the amount of water manufactured in the body of a kangaroo rat is neither more nor less than of a meadow mouse of equal size fed an identical diet, unless there might be a differential rate of the basic metabolism.

Water is given off from the body in three ways; in the form of water vapor in respired air; in the form of sweat through the sudoriparous glands of the skin; and in the form of urine, or to some extent, of course, in moist feces. It is only by modifying these three physiologic processes that a mammal can contrive to conserve the water that its body contains. The fact that at least some of these rodents will partake of water when it is offered them, or seem to remain indifferent to its lack when it is withheld for months at a time, suggests that their excretion of water varies within fairly wide limits, dependent upon the moisture content of the body.

But little or nothing is known regarding the functioning of the sensory equipment of the kangaroo rat. Its infraorbital tactile sense, through the vibrissae, is certainly keen, but probably to no greater degree than in many rodents. Its large eyes denote good nocturnal or crepuscular vision, but whether this sense is depended upon to a greater degree than that of smell is a question. But one may safely say that the acoustic sense is extremely highly specialized in this rodent. Unfortunately we have no inkling of the precise, or even approximate, quality of hearing involved, for the acoustic apparatus differs from that of man in a number of features and thus it may involve factors of which we have no conception. The only opinion that I have had on the subject is that the kangaroo rat places great dependency upon resonance or vibrations through the ground—or in other words that its enormous, hollow bullae act as sounding boards—and perhaps less upon air borne sound waves than the majority of mammals. Thus an individual may quietly be fol-

lowed, in the light of an electric torch, within three or four feet as it forages here and there. It will remain indifferent to conversation or other noises if of not too sudden a nature, even when these are rather loud. But the slight tap of a pencil upon the ground will send the subject out of the picture in a single bound. It is thus inferred that the genus is particularly alert for the detection of the light footfalls of its enemies, which must often approach unseen behind the shelter of the scattered desert brush.

In progressing at a deliberate pace the kangaroo rat employs the creeping gait of the majority of rodents, with the tail dragging behind. This is a walk, the fore feet being always employed; but during the frequent pauses the fore feet are elevated and the body is then supported solely by the hind legs, unless the posture involves the placement of the nose close to the ground. When exploring new surroundings, after being liberated in a large box or a room, *Dipodomys* appears to be more prone to stretch upward on its hind legs while steadied by its tail, for the purpose of testing and smelling the walls above its head, or rather to indulge in this action more frequently, than are the majority of rodents. This is doubtless for the reason that the shorter body and more powerful musculature of the posterior limbs facilitates this action, and it is thus more naturally indulged in.

Only rarely have I observed this animal to progress at slow speed by any gait other than a walk, and this has consisted of a slow hop, involving the placing of the fore feet upon the ground followed by the forward movement of both hind feet in unison. When moving faster than a slow walk the animal hops, bird-like or kangaroo-like with tail held stiffly to the rear, the distance between foot prints varying with the speed. When this measures some two or three feet the actions are graceful, the tail then acting as an effective equilibrator and all of the movements of the animal appearing to be in perfect coördination. When panic increases the length of the leap to the neighborhood of six or eight feet the speed of the animal would seem to exceed its control. At least it has been my experience that it is then likely to make a rather poor, unbalanced landing, and that before full recovery has taken place a powerful kick by the hind feet will often send the animal hurtling through the air once more in a more or less lopsided fashion. If in an especial hurry it may thus fail to plan its course with proper foresight and occasionally will land amid the dense twigs of a small shrub in anything but a tactical position.

Perhaps, however, this tendency to leap anew before a perfect

balance has been recovered after a hop has a certain advantage. For one thing it lends to the swift progression of this animal a certain erratic quality that must be exceedingly confusing to an enemy. This is further enhanced, at the will of the individual, by the fact that the tail is a very effective rudder. Its proper use will correct, in the midst of a trajectory, any error of balance caused by a faulty "take-off," and it must enable the animal, when closely pressed, to execute the marvelous dodges for which it is famous, and which are the despair of a pursuer. When chased by a dog (or other enemy) and hard pressed, the kangaroo rat will perform a series of right-angled zig-zags involving such abrupt changes of direction that the dog is reduced to complete helplessness. In fact it is likely that no mammal can catch this rodent in fair chase, but only by stealth.

The long tail of *Dipodomys* is subject to many vicissitudes and individuals having this member considerably shortened are frequently secured. If the loss be considerable in amount the animal is much handicapped in its long leaps and will frequently turn completely over in midair.

Whether the speed of these rodents in a linear sense would compare favorably with that of a rabbit, for instance, is questionable. I regard their long hind limbs as not remarkably serviceable in this regard, but rather that they have been developed for giving considerable speed with phenomenal dodging ability, as well as rather high cruising speed for the purpose of covering a considerable amount of territory in search of food where this is often scarce. The distance that it is possible for them to cover at a single bound remains to be determined. I have endeavored to ascertain this but have been unable to do so to my satisfaction. I think it doubtful if it is possible for them to cover more than about 12 feet, with a lesser distance for the smaller species.

There here intrudes the question of whether the gait of the kangaroo rat is digitigrade or plantigrade. At slow speed the latter is the case, although it is prone to stretch upon its toes to investigate an object above its head. At cruising speed it is digitigrade to a considerable extent; but so are many mammals that are classed as strictly plantigrade. Even man is digitigrade when running rapidly and the same may be said of *Dipodomys*. The final impulse for a leap is furnished by the toes, and the animal may even land on the toes, without the heel touching the ground.

The characteristic sleeping posture of *Dipodomys* is, like most rodents, resting on the heels with the head and nose tucked beneath

the belly, at times with the forehead actually resting upon the ground, but occasionally a sleeping captive will be detected sprawled upon its side. When at perfect rest or dozing the weight of the animal will be rested squarely on the heels, but when on the alert and ready for action, but still motionless, the center of gravity is shifted forward over the metatarsi (fig. 3).

HABITS OF THE JERBOAS.

But few accounts of the habits of the jerboas are available and these are anything but satisfactory. For the following notes on *Scirtopoda orientalis* I am indebted to the late John Hornung, the collector of my specimens. He related to me that near Alexandria the species is common throughout stretches of aeolean sand but does not occur upon heavier soil. Thereabouts there is so little vegetation, and this is so scattered, that it is difficult to understand how the animals subsist, even though the length of their legs fit them well for covering long distances. Their burrow systems are quite extensive but very close to the surface; hence one may insert his hand in a burrow and with his arm "plow" along until the inhabitant is reached. Arab boys capture numbers in this way, and while endeavoring to dash past the hands of their pursuers, the animals often dart up the capacious sleeves of the native costume, from which they are easily extracted unharmed.

Clark and Sowerby (1912), have stated that the Chinese 3-toed jerboa *Dipus sowerbyi* is a purely sand-loving animal, inhabiting the dunes which exist in and on the borders of the Ordos Desert. Its burrows are almost impossible to find and it is a question whether it fills up the mouths of these purposely or whether this is accomplished naturally by the loose sand. At the time of their visit it was too late in the year to investigate this point as the jerboas were hibernating. From the tracks it was judged that they can leap for a distance of 8 feet. When asleep they lie upon their sides for the better accommodation of the long hind legs. When proceeding slowly they hop upon all four feet, but when progressing at some speed the hind limbs are employed exclusively. The present writer is of the opinion that the above figure of 8 feet refers to the average distance covered by each leap when the animal is progressing at reasonable speed, but that in sudden panic a considerably greater distance can undoubtedly be covered.

Blanford (1888), in writing of a genus of a much lesser degree of

saltatory specialization, has stated that *Gerbillus* can cover a distance of 4 or 5 yards at a single bound.

Very little is known regarding the habits of the Chinese *Allactaga*. Sowerby (Clark and Sowerby, 1912) stated that it is not so essentially a sand-inhabiting animal as is *Dipus sowerbyi*. Captive animals sleep upon the side or back and if disturbed kick and bite savagely. When not on the alert they have a queer habit of drooping the terminal half of the ears.

From the meager references to the character of the habitats of the more saltatorial form of the *Dipodidae* it seems safe to state that their distributional preferences are almost identical to those of *Dipodomys*, save that they appear to be more strictly confined to a steppe or desert type of country, seeming to shun brushy surroundings such as at times harbor the kangaroo rat in numbers. This is to be expected in connection with the greater saltatorial specialization of the Asiatic animals.

One of the most interesting points in regard to the habits of the jerboas is concerned with the degree to which they are digitigrade. It seems to me clear beyond question that during slow progression all four feet are employed, and this contention appears to be substantiated by photographs. Even so, the extreme length of the hind limbs must prove a definite handicap during the creeping tactics employed by all rodents in searching for small fallen seeds. John Hornung has assured me that in captivity *Scirtopoda* is even more prone than is *Dipodomys* to stretch upward upon its toes, while using its tail as a third member of a tripod, for the purpose of investigating everything within reach, and in the wild this ability must be put to practical use in aiding the animal to secure seed pods that would otherwise prove unattainable. At considerable speed the jerboas are, beyond question, digitigrade, just as are kangaroo rats, but undoubtedly to a more pronounced extent, utilizing the longer pes for imparting an augmented thrust to the long legs.

EXTERNAL CHARACTERS.

Measurements and Weights.

Except in the case of foot length, reasonably satisfactory external measurements can be given only for those species listed below, for skins of these are available and measurements were made from the fresh specimens by the collectors. The dimensions, in millimeters, of two specimens of each are accordingly given, and those of the large *Dipodomys deserti* are also included.

	Head and Body	Tail	Pes
<i>Dipodomys spectabilis</i>	136 and 140	190 and 210	50
<i>Dipodomys deserti</i>	136 and 145	214 and 225	55 and 60
<i>Allactaga m. longior</i>	134 and 138	209 and 205	69.5 and 71
<i>Dipus sowerbyi</i>	116 and 120	160 and 176	62 and 66

It was found that because of the difficulty in correctly allowing for the curve of the vertebral column in the hardened alcoholic preparations the relative proportions of the spirit specimens of *Allactaga* were so at variance with those of the study skins that I am loath to place any dependence upon the head and body measurement of *Scirtopoda*, taken from alcoholic specimens only. In the latter animal, however, the body appears to be relatively a bit longer, and the tail slightly shorter, than in *Allactaga*, while the foot is about the same.

A freshly caught specimen of *Dipodomys spectabilis* weighed 124 grams, and four years later when removed from spirits and allowed to drain for a few minutes, 135 grams. It had thus absorbed moisture to the extent of about 9 per cent of its original weight. On this basis a specimen of *Scirtopoda* before me, weighing 132 grams, must have tipped the scale when freshly caught at about 121 grams; and an individual of *Allactaga*, 106 grams. It is thus seen that the specimens dissected were as nearly similar in size as one could reasonably wish.

Head.

In considering the external characters of the three genera dissected account will also be taken, where it seems desirable, of the features of other saltatorial mammals, but only briefly, because many sorts have not been available for examination, and some of those seen have been in an unsatisfactory condition for proper study.

In saltatorial rodents the external ear conforms to two general patterns. At one extreme there is the phenomenal pinna of *Euchoreutes*, comparable in some respects to that of the desert hares, and at the other the small type of pinna of the sort encountered in kangaroo rats and mice and some jerboas. It is the rule that a large pinna accompanies an auditory bulla that is not unduly inflated, while a small pinna upon a mammal highly adapted for saltatorial progression indicates an enormous bulla. But there are exceptions to this rule, at least to the extent that two 3-toed jerboas with approximately equal development of the bulla may have the pinna either almost as short as in *Dipodomys* (i. e. *Dipus sowerbyi*) or considerably longer,

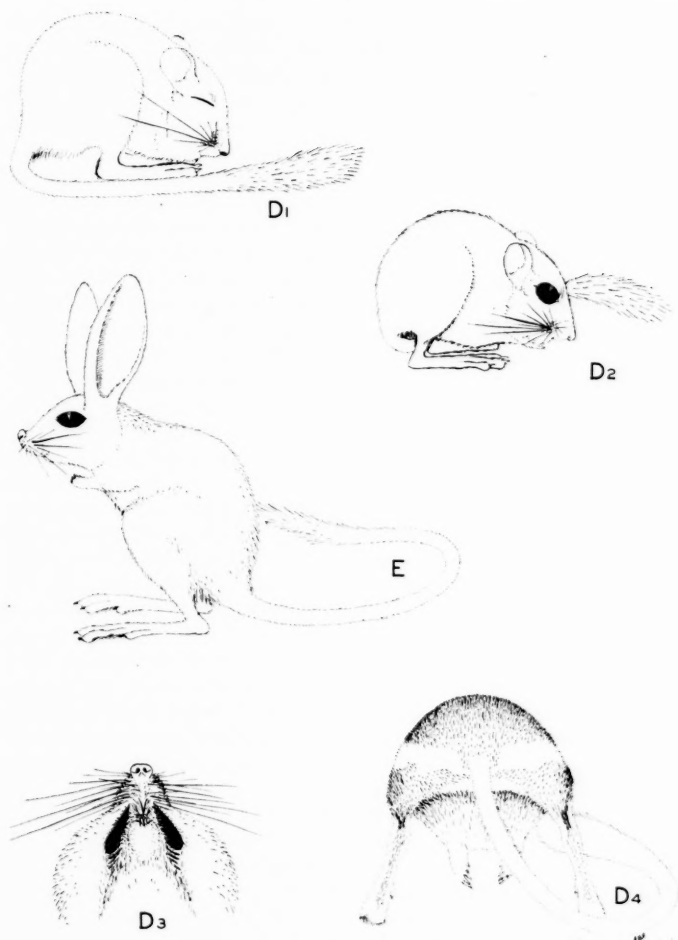


FIGURE 3. Postures and proportions of *Dipodomys* (D) and of the Asiatic *Euchoreutes* (E). D₁, lightly dozing, with center of gravity over heel; D₂, alert, with center of gravity over base of toes; D₃, openings of external cheek pouches, the latter represented as filled; D₄, typical digging posture. Shown without regard to uniform reduction.

as in *Scirtopoda*. But I know of no case in which an animal has both a long pinna and phenomenally inflated bulla.

Grinnell (1922) has called attention to the fact that within the genus *Dipodomys* "Consideration of habitats in connection with size of ear brings out unmistakably the correlation of small pinna with open type of habitat, and, in the other direction, of large pinna with a chaparral type of habitat. The same tendencies are to be observed in *Peromyscus* and *Perognathus*." The same author has further stated that "An interesting circumstance, however, with *Dipodomys* at least, is that, in many of the small-eared forms, the relative inflation of the mastoid and tympanic portions of the skull is far greater than in the large-eared forms. Increased effectiveness of the internal parts of the aural apparatus would here appear to be in some measure compensatory to the reduction of the external parts. There are apparent outstanding exceptions to the above rule of compensation, however."

In *Dipodomys spectabilis* the length of ear (in an alcoholic specimen) measured from the crown was 10, and from the notch 17 mm., with a width of 10 mm. The pinna was blunt and evenly rounded and the anterior border was folded back so as almost to hide the base, which was not tubular. The antihelix (Pocock's supratragus) was well marked and the antitragus was distinct, although not much developed. The tragus was absent as a true prominence. In this species the ear was covered with fine hair but there were no marked fringes to the border. No color pattern was apparent, although Grinnell (1922) has described and figured considerable variation in the auricular color plan in the different species of the genus, this being for the most part a basic pattern of darker distal and paler proximal parts, varying in intensity of tone according to the shade of the body coat. This general style of pinna is characteristic of the Heteromyidae.

Illustrations clearly show that the ears of the smaller of the two species of Egyptian jerboa (*Dipus jaculus*) are of the short type, apparently rounded much as in *Dipodomys*, and this also appears to be the case in the little Asiatic *Salpingotus*, with its enormous bullae. Perhaps the pinna of *Dipus sowerbyi* and its close Asiatic relatives should also be classed as short, for it measures 13 mm. from the crown and 17 from the notch; but it is considerably more pointed than in *Dipodomys*.

Pocock (1922) has stated that in *Scirtopoda* the ear, when laid forward, overlapped the eyes by a little. In my alcoholic specimens

the ear reached half way from the eye to the nose, measuring 27 mm. from the crown and 30 from the notch, with a width of 13 mm. It was tubular at base and the antihelix was poorly defined except when the ear was laid back, when the cartilage became creased at this point. In fact this may always be regarded merely as a cartilaginous hinge. There was really no tragus defined, at least in its normal situation, although an inner fold near the base of the anterior border may well be homologous with this prominence. Although the ear was so much longer than in *Dipodomys* the distal border was hardly more pointed. The pinna was scantily covered with exceedingly fine, short hairs, as is usual in mammals, and in addition the anterior border was well fringed, these hairs being longer and more plentiful toward the base; and the base of the posterior border was also rather densely haired.

Pocock's illustration indicates that the ear of the four-toed African *Scarturus* is relatively longer and more pointed than in *Scirtopoda orientalis*, but not to the extent encountered in *Allactaga*. Pocock stated that in the species *indica* of the latter genus the ear reached about to the end of the muzzle, but in the alcoholic specimens of *A. mongolica longior* available the distance so reached was slightly more than half way from the eye to the nose. From the crown it measured 32 mm. and from the notch 34, with a width of 13 mm. It tapered more toward the tip than in *Scirtopoda* but was also tubular at base, with the anterior border more folded. The fold upon this border that may represent the tragus was smaller and hidden within the conch, and the antitragus, while small, was better defined than in *Scirtopoda*. There were two antihelical folds and the hairs were distributed more plentifully than in the 3-toed animal.

The external ear of *Euchoreutes* is relatively more developed than in any other living mammal, with the exception of some bats, and reaches well beyond the nose when laid forward. It is really astounding in its proportions (see fig. 3), but only a dried skin in poor condition is at hand and little or nothing can be told regarding its detail, save that the border fringe is very well developed.

The ear of *Pedetes* is also of the long type and is highly specialized (fig. 4). Pocock found that apparently at the will of the animal the ear can be folded lengthwise so that the anterior and posterior borders are in contact, while a slender process at the base, which seems to be a specialized tragus, fits between them. The antihelix or supratragal ridge extends lengthwise of the pinna so as to facilitate closure.

Sowerby found that when the Chinese *Allactaga* was not on the alert it had the odd habit of drooping the terminal half of the ears.

At least in the alcoholic specimens examined, and presumably in all saltatorial rodents that live in burrows amidst a desert habitat, it is apparent that when the ear is retracted the inner folds and prominences dove-tail into one another so as to effect practical closure, and thus exclude particles of fine sand. This is also facilitated by the marginal fringes.

In almost all rodents the eyes are so situated that the animal can see in every direction without movement of the head, but we know nothing whatever about the quality of vision concerned. In all certainty stereoscopic vision, of the sort characteristic of man, does not exist in rodents, but there is an effective binocular panoramic vision.

Size of eye is a criterion of an animal's habits, but the interpretation of this detail is not always easy. Thus an eye of moderate size may mean that an animal is diurnal with keen vision, or nocturnal and with rather mediocre sight. In rodents a difference of a couple of millimeters means little when tabulated, for it is almost impossible to compare this detail properly with body size, and so obtain uniform results. But after making observations I am of the opinion that all saltatorial mammals have rather large eyes, this possibly being mainly attributable to uniformly nocturnal habits, save to some extent in the case of the lagomorphs or hares. In species but slightly modified, and usually of small size, which must depend more upon caution than speed to escape from enemies, thus being more prone to forage near protective vegetation, increase in the size of the eye is not marked, while in the more specialized sorts, whose ability to leap and dodge enables them to range well into the open with reasonable safety, the eye is inclined to be larger.

In those animals dissected the distance between the canthi of the eye was 9 mm. in *Dipodomys* and *Scirtopoda* and 8 in *Allactaga*, while in a small wood rat (*Neotoma*) of comparable size this measurement was less than 7 mm. In all of these the center of the eyeball was about 60 per cent of the distance between the nose and the notch of the ear, save in *Scirtopoda* with its short muzzle, in which this percentage was 55.

In these saltatorial rodents there is a relative increase in the distance between the eyes. In a specimen of *Neotoma* this distance was but 43 per cent of the head length, while in *Dipodomys* and *Allactaga* this item rose to 61, and in *Scirtopoda* to as much as 76 per cent. It

seems, however, that this eye width is more strongly determined by such considerations as are influenced by inflation of the audital bulla than by any purely visual requirement.

The most interesting ocular detail from the present viewpoint, however, is in the angle at which the eye is set. After having borne this question in mind for a number of years I have been led by numerous observations to believe that in mammals the eye is so situated that in the posture in which the animal most often carries its head,

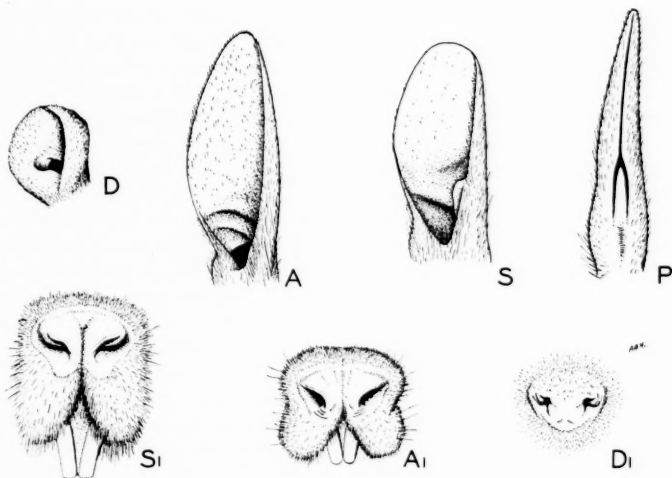


FIGURE 4. Right ears ($\times 1$) and rhinarial region ($\times 2$) of *Dipodomys* (D) *Allactaga* (A), and *Scirtopoda* (S). The ear of *Pedetes* (P), redrawn from Pocock, is shown in the closed position, supposedly peculiar to this genus.

or let us say in the posture of the head during its most critical activities, a line drawn between the canthi will be to all intents horizontal with the ground. So far as I know this detail has received no previous consideration, but it is a development that would be entirely logical, enabling the greatest possible breadth of vision to be attained. It seems then that this is a valuable index to the angle at which the head is normally carried. Employing it thus it has been found that in a wood rat this line through the canthi forms an angle of 15 degrees

with another line stretching from the tip of the nose to the notch of the ear. Although the latter is not the precise axis of the skull it is here so considered for convenience. Thus the wood rat can be judged to carry its head depressed to an extent of only 15 degrees from the horizontal. In *Dipodomys* this angle of deflection was found to be 32 degrees, in *Sciurtopoda* 40, and in *Allactaga* 50 degrees. In the wood rat it is impossible to decide whether the need for widest vision, or in other words the determinant for canthi angle, is experienced while the animal is sneaking through dense vegetation on the watch for enemies, or while searching for seeds on the ground beneath. In the jerboas and kangaroo rats, however, it is apparent that greatest keenness of vision is not needed so much when the animal is in full flight, but rather when it is quietly going about its business, nose to ground, either for finding food or with a wary eye watching for enemies.

In *Dipodomys* some of the mystacial vibrissae are as long as 75 mm., and these are black, while the shorter ones, located farther forward, are white. There are also two or three superciliary vibrissae, but no others could be found. Over the face, however, and especially below the eyes, the guard hairs are very long, and these doubtless have some tactile function. In *Allactaga* the longest vibrissae were about equal to conditions in *Dipodomys*, but in *Sciurtopoda* they were slightly longer (82 mm.). In both the vibrissae were entirely black at base, although a number had white tips, and in *Dipus sowerbyi* there was more white. The two or three most ventrocaudally situated were the longest, and also stouter than the rest. Two or three superciliaries were present and nearer the eye a number of black bristles, 6 or 8 mm. long, more plentiful upon the lower lid. These were more scanty in *Dipus sowerbyi*.

In *Dipodomys* the nose had no differentiated rhinarium and as the tip was approached the hairs of the rostrum became progressively shorter until upon the nose proper they were exceedingly short, and white. The borders of the nostrils were somewhat folded so that complete closure, while digging in loose sand, should be easy of accomplishment. There was no sharp philtrum or medial groove, although this was slightly indicated. In *Sciurtopoda* there was a well differentiated rhinarium, abruptly hairless. The nostrils were of scroll shape, on the same general principle as, but of a different shape than, those of *Dipodomys*, and there was a deep philtrum which tended to branch above the nostrils. In *Allactaga* the scroll-like part of the nostrils was more deeply situated so that it was less apparent, the philtrum did not divide above the nostrils nor was

the nasal part quite so deep, and there was a slight lateral depression between the nasal and labial parts of the muzzle. In the single study skin of *Euchoreutes* which I have examined the nose appears to have dried in a position that is relatively undistorted. In detail it is considerably different from the other jerboas discussed for there is a raised terminal border, which gives it the appearance of being the snout of a minute pig.

Although in *Dipodomys* there is no well marked labial philtrum, the upper lip is divided so as to form a slight inverted V, and there is therefore no maxillary oral vestibule. The bases of the mandibular incisors are ensheathed by a labial fold and here there is a vestibule a couple of millimeters in depth. Lingual cheek pads in the region of the diastema act so as to close the mouth completely posterior to the incisors as in many other rodents. The opening of the external cheek pouches is parallel to a line passing from the nose to the undershot chin and is about 20 mm. in length, varying in precise position and measurement according to the position in which the specimen was fixed by the preservative. The cheek pouches are about 35 mm. in depth but are capable of considerable stretching. The upper part of the opening is situated opposite the base of the maxillary incisors, and the lower angle far beneath the chin. The lateral lips extend uninterruptedly into the pouch, which is lined with sparse, short, white hairs. It appears from both superficial and myological examinations that these pouches have always been external in situation since their original inception, and not that they have developed from any sort of internal pouch as now found in squirrels, hamsters, etc.

In *Scirtopoda* there is a deep labial philtrum and the cleft character of the upper lip is much more marked than in *Dipodomys*. The mandibular vestibule is as deep as 7 mm. and closure of the mouth is effected more exclusively by the posterior part of the upper lips, or rather, the chief action of the lingual pads is more dorsal, so that after closure the orifice of the mouth may be compared to the letter T rather than to a short vertical line as in *Dipodomys*. In this animal the hairs of the upper lip bordering the incisors are very long. In *Allactaga* conditions are largely the same, but the maxillary incisors are more projecting and the lower ones longer, giving space for longer lingual cheek pads which appear to be less efficient in their valvular action.

Body.

Character of pelage as well as pattern was determined by observing alcoholic specimens immersed in a dish of water, as well as study skins.

Although a large part of the range of *Dipodomys spectabilis* is arid desert this species is but little paler than many non-desert rodents, and much darker than the excessively pale *Dipodomys deserti*, whose range immediately adjoins, and perhaps overlaps, that of *spectabilis*. But it is very much paler than many species inhabiting more humid districts. *D. spectabilis* is slightly darker than *Dipus sowerbyi* and *Scirtopoda orientalis* in its darker pelage. It is, however, considerably paler and less sooty than *Allactaga mongolica*. One of the specimens of *Scirtopoda* was in changing pelage, the shorter part, evidently comprising patches of the summer coat, was almost as pale as *Dipodomys deserti*, which is one of the palest rodents in existence, while the longer patches, evidently of the winter coat, were practically as dark as is *Allactaga* but more ochraceous. The character of the pelage of *Dipus sowerbyi*, *Allactaga mongolica*, and of the dorsum of *Scirtopoda orientalis* is not noteworthy, fluffing out in water to the same degree as in most rodents. The entire pelage of *Dipodomys* of all species, and of the thighs, lower shoulders and much of the underparts of *Scirtopoda*, however, is particularly lax, long, and appearing as though slightly matted by grease. That this is characteristic of the pelage regardless of its condition is certain, but when live *Dipodomys* are deprived of fine sand in which to dust and cleanse the fur the condition becomes aggravated by the products of the skin glands and the animals then present an unkept, bedraggled appearance.

Many species of leaping mammals, including the lagomorphs, have an unusual amount of ochraceous coloration in their pelage, this often being intensified over the sides to almost an apricot shade. But this is attributable to the fact that very many of the saltatorial species are inhabitants of desert areas, where paleness and brightness of pelage are a corollary of arid climatic environment, and their near relatives of more humid regions are darker and duller. In the pattern of the coat markings, however, saltatorial rodents are prone to exhibit a noteworthy degree of convergence. White underparts are too uniform among mammals in general to deserve more than mention, but there is a tendency, although this is not by any means invariably shown, for there to be whitish areas between the nose and eye, above the eye, and at the base of the ear. More remarkable is the tendency to develop a broad and abruptly white stripe extending from the base of the tail to the thigh. Apparently this is present in all kangaroo rats and all jerboas, although not in the kangaroo mice nor in mammals of minor saltatorial development. This seems not to be so strictly an independent white marking, but rather that the white of the under-

parts extend thus high upon the flank, while the darker coloration of the upper parts have secondarily invaded the thigh. In some specimens of *Allactaga*, but not in others, the white of the flank is bordered below by long black hairs (frontispiece). The result of this uniformity of color pattern, including that of the tail, in connection with the similarity in bodily conformation, results in the fact that in regard to general external features the peculiarities that have been developed by the kangaroo rats appear almost exactly to match those of the unrelated jerboas. Included in these features are apparent shortness of body and relatively large head, as well as the fact that following the development of the fore and hind limbs, the posterior part of the body is heavier than the anterior; but these details will be discussed more fully in connection with the osteology.

Attention should be called to the presence in *Dipodomys* only, among the Heteromyidae and other saltatorial mammals, of a small cutaneous gland situated mid-dorsally and slightly posterior to the shoulder blades. This is of about the same size as the ocular aperture, is hairless, granular or warty in texture, and stands slightly above the surface of the skin. It is probably a scent gland but extrudes no apparent exudation and the surrounding hairs are always dry. That a gland should have developed upon the back or sides is not surprising, but it is somewhat remarkable that glands in this precise situation should have been acquired by the unrelated ground squirrels of the genus *Callospermophilus* and at least some species of African hyraxes (Hyracoidea), of ungulate affinity. Presumably these glands serve to scent the top of the burrows through which the animals pass.

The mammillary formula of those species of *Dipodomys* examined for this feature is two pairs inguinal and one pair pectoral.

In saltatorial mammals the tail has the double function of equilibrator during speedy progression and as a third leg or prop while a bipedal posture is assumed. Hence it is directly dependent in considerable degree upon length of hind limb, or in other words, leaping ability. The tendency as specialization advances is undoubtedly for an increase in length of tail and acquisition of a terminal tuft or brush, which usually becomes black in color at some later stage, and ultimately may be expected to acquire an abruptly contrasting white tip.

In many of the pocket mice of the genus *Perognathus* the tail is actually shorter than the head and body, reflecting the tendency for generalized, non-leaping, non-climbing desert rodents to have shorter tails than their relatives of less arid regions. In no *Perognathus* is the tail much more than one fifth longer than the head and body,

and this is no longer than in many of the spiny heteromyid mice of non-saltatorial propensities from Mexico and farther south. In the shorter-tailed pocket mice there is no terminal brush developed by the tail, nor is this present in the kangaroo mouse (*Microdipodops*) whose tail is but little longer than the head and body. In pocket mice with longer tails the terminal pencil is usually present and entirely of a color with the remainder of the dorsal aspect of the tail. In some species of the Old World genus *Gerbillus* the tail is also pencilled and in others not. In at least some species of the partly saltatorial genera *Taterillus*, *Dipodillus*, *Meriones* and *Rhombomys* the terminal tuft is darker than the rest of the tail, and this becomes virtually black in *Pedetes*, some species of *Tatera*, and some of the Allactaginae, while there is an abruptly white tip to the generally black pencil in most of the highly saltatorial jerboas. Apparently in the latter animals this white tip is acquired by the gradual spread of a terminal area in which each hair is completely white. In *Dipodomys*, however, I judge that the development of this detail is on a different plan.

In some of the paler races of *Dipodomys* the brush has neither black nor white areas, but the color is the same as the rest of the dorsal caudal surface, while in some of the darker, smaller sorts the tail is uniformly sooty above. From this a white tip seems to be formed, in those that exhibit this character, not by the progressive encroachment of an abruptly white area, but by the gradual extension distally of the white bases of individual hairs. This process, clearly illustrated in some forms, possibly may not have taken place in a few exceptions, such as in *D. spectabilis*, for here the white tip is as abrupt as in any jerboas. In its greatest development the caudal hairs begin to lengthen at the middle of the tail or even proximal to this point. In the Heteromyidae the dorsal hairs are the ones that show the first and greatest development, although those of the side are later involved also, while in the jerboas the lateral hairs are the ones chiefly concerned, giving to the tail a somewhat feathered effect. In *Dipodomys* the basic tail pattern is quadriform, the sides being white and the dorsal and ventral borders darker. In a form as pale as *D. deserti* the ventral stripe is very narrow and faint, having disappeared in a few specimens, while the proximal part of the dorsal stripe is of a very pale salt-and-pepper effect, but in darker species both of these stripes are sooty, and these may be broader than the lateral white ones which separate them. In the jerboas, however, the proximal part of the tail is bicolor, buffy above and white below. The latter

may extend entirely to the tip, or else be practically eliminated where the black hairs of the pencil encroach ventrally.

Mention may here be made that frequently one finds in his traps specimens of *Dipodomys* whose tails have been shortened through accident. If the condition of the stump suggests that this took place at some considerable time in the past, there will likely be present at the tip an accessory tuft of hair that is more abruptly defined, of lesser extent, and composed of longer, more bristly hairs than was the original. This, clearly, is an effort on the part of a damaged tail to regenerate a detail that is of much importance in the animal's economy.

There is considerable variation in relative length of tail within the genus *Dipodomys* and at present this cannot be correlated with other features. Grinnell (1922) has stated that "the average ratio of tail to body in 33 California forms is 145 per cent. . . . The two extremes in the averages are 116 per cent and 167 per cent for *monoensis* and *californicus* respectively." But "In so far as the writer can see there is no significant correlation between either length or slenderness of tail with size of hind foot, with presence or absence of first claw on hind foot, with size of ear, or with geographic distribution." An attempt to determine from my alcoholic specimens the percentage of tail length to the length of head and body proved somewhat unsatisfactory because of the cramped position of the hardened bodies. But judging by the collectors' measurements on study skin labels the tail in these rodents is close to 150 per cent of the head and body length (*Dipodomys spectabilis*, 140-150; *D. deserti*, 155-157; *Allactaga*, 148-155; *Dipus sowerbyi*, 138-147; *Zapus*, 143). Judging by alcoholic specimens the tail of *Scirtopoda orientalis* is certainly no longer than that of *Allactaga m. longior*, and appears to be shorter.

From an examination of the animals studied in the present connection it would appear that there is no alteration in the diameter of the tails of these highly saltatorial mammals, for in this feature they are strictly comparable to rats of about equal bulk. Grinnell (1922), however, found that among the California forms of the genus there is variation in the thickness of the tail, to the extent that freshly caught specimens, of about the same size but representative of different groups, may be distinguished by this feature alone. "*Merriami* apparently exhibits the slender extreme of this genus (within the state), while the opposite obtains in *ingens*."

The tails of the lagomorphs, or hares and their allies, are not comparable with those of jerboas and kangaroo rats. Their tails

are vestigial and non-functional, in the little pikas as well as the big desert jack rabbits, and they were probably in this condition before the latter animals developed marked cursorial and leaping ability. A tail that has thus been reduced to a vestigial condition appears utterly unable subsequently to attain to respectable proportions.

There are many factors which affect the conformation of the feet of rodents. In the majority the fore limbs have two critical functions, consisting of those concerned with feeding activities, and those connected with locomotion. In the genera in which the hind limbs have developed so that speedy progression is accomplished by saltation, the second of these functions has been abandoned, and the critical role of the fore limbs comprises their use as hands, with support of the anterior body relegated to a secondary position. The result, apparently, is a decrease in the robustness of these members. Whether they also become shorter depends upon feeding requirements but not, directly, upon any corollary change in the length of the hind limbs. In other words it seems quite certain that elongation of the hind limbs can not, per se, effect any compensational shortening of the fore limbs.

In *Dipodomys* the pollex is a mere rudiment with a short, very blunt nail. The other nails are long (5.5 mm. in the third) and taper very little. Digit 2 is slightly shorter than 4, which is practically as long as 3. The metacarpals appear normally to be held over-extended so as to form with the forearm an angle of about 45 degrees, while the nails are at the same time flexed to form an angle of 90 degrees with the metacarpals. This is so in the preserved *Scirtopoda* also, but in *Allactaga* this respective extension and flexion is much less pronounced. There are slight transverse creases upon the palmar aspect of the digits of all three animals, as is so often the case in rodents, and there are fine papillae upon that part of the distal palm that is not covered by the pads. There is a very small but high tubercle just posterior to and fairly between digits 3 and 4, and another at the ulnar base of 5. There are two main palmar pads, large and high, but not quite as sharp as in the jerboas. The more radial one is partially double, and the other has a row of short hairs extending obliquely distally from the wrist (fig. 5, D1). As in other rodents similarly equipped these pads function in a manner comparable to the human thumb in aiding the digits to grasp objects which the animal desires to handle. There is no differentiated carpal vibrissae area, but the hairs over the wrist are quite long, moderately stiff, and must have some tactile ability.

In a fresh specimen of another species (*Dipodomys agilis*) the manus was found to be highly mobile, with possible pronation to about 75 degrees, and supination through the joint and the bones of the forearm to at least 150 degrees.

The nail of the pollex of *Scirtopoda* is heavier and longer than in *Dipodomys*, but still very blunt. The other nails are about of equal length (5.9 mm.) but more tapering. The palmer surface of the digit is finely haired, which is not the case to an apparent degree in *Dipodomys*, and the distal palm is without fine papillae. To all intents there is but one large and very high pad, partially divided by a crease and with the anterior border somewhat irregular. The carpal hairs are much as in *Dipodomys* but in addition there is a differentiated carpal vibrissae area near the wrist.

In the two above animals the nail of the pollex is slightly worn, but in *Allactaga* it is unworn and conical, so I judge that the growth may be slower and that it is even more rudimentary. The other nails are a bit shorter (4.3 mm.) and are tapering, and the palmer surface of the digits is marked by transverse ridges more faintly than in *Dipodomys*, and like the latter there are two small but high tubercles upon the distal palm similarly situated, and two large and high palmar pads as well. There is no differentiated vibrissae area upon the wrist.

In *Scarturus* there are said to be three tubercles, but only two in *Euchoreutes*, according to Pocock, who also found that in *Allactaga indica* there was but one. In most jerboas the nail of the pollex is blunt, but in *Euchoreutes* it is clawlike and as in the other digits, and this is also the case in *Pedetes*, the especially large palmar pads of which were considered by Pocock to have the ability of independent movement. The possibility of the latter feature is very doubtful because of the impracticability of the development of controlling musculature.

In reporting on the wood rat the foot length compared to that of head and body of the specimens whose measurements were given varied from 17.2 to 20.2 per cent according to species. For *Dipodomys* I have determined this percentage by taking average measurements as given by Grinnell (1922) for all (16) of the full species which he listed, and added to them those of *D. spectabilis* and *D. gravipes*. The average for the entire lot was 33.4 per cent, varying from 37.7 for the small *D. nitratoides* and the medium sized *D. agilis*, and 37.6 for the large *D. deserti*, down to 34.7 for *D. ingens* and 33.8 for *D. gravipes*, both large species. The foot of *D. spectabilis* is somewhat

above the average, being about 36.5. In the American jumping mouse *Zapus* the percentage is about the same as the average for the kangaroo rat, or 33.

But the above figures do not tell the whole story, for *D. gravipes* has a foot that, although short, is particularly broad and heavy, while in other sorts the foot may be relatively narrow. Thus, in speaking of the California races, Grinnell (1922) has stated that the pes in "the *merriami* group shows an extreme of slenderness, while the *heermanni* and *agilis* group shows an extreme of heaviness (that is, the foot is relatively broad). There is a fairly clear correlation here with existence on bare, open ground sparsely grown to vegetation, as compared with more or less grassy or bushy territory. The slender-footed *merriami* group is most abundant as to individuals on the most open ground. If "broad-footed" groups are represented in the same general vicinity, they will be found to predominate on ground of the opposite characteristic."

For the jerboas whose skins are available the percentage of foot length to that of head and body is 41 for the little *Euchoreutes*, 52 for *Allactaga*, and 54 and 55 for *Dipus sowerbyi*, according to collector's measurements. Thus the relative size of hind foot compared with length of head and body averages for the wood rat, kangaroo rat, and jerboa, respectively, about 18.7, 33.4, and 50, or expressed still more roughly for convenience, as the numerals 4, 7 and 10 compare with one another.

As compared with the foot of *Neotoma* that of *Dipodomys* is both relatively and actually less broad, the proximal part of the sole is greatly elongated and the distal part (area of palmar pads) much reduced. Whereas in *Neotoma* the length of the third toe without its claw, measured on the longer, medial side, is one-fifth of the total foot length, in *Dipodomys* it is one-quarter, showing that the toes have increased in length even more rapidly than the rest of the foot. The relative proportions of the four lateral toes have suffered no alteration, however, save that digit 5 appears to be very slightly more reduced than in *Neotoma*. Some species of *Dipodomys* entirely lack an external hallux, some are variable in this respect, and others normally have this toe represented vestigially, it being either entire or with the claw and terminal phalanx lacking. But this will be further discussed elsewhere.

The whole sole has the skin in a faintly scale-like pattern and the plantar aspect of the digits is transversely creased. The plantar pad area is not sharply marked but consists only of an irregular promin-

ence of the sole near the base of the toes. The juncture of digits 3 and 4 is situated farther distally than those of the others. Hairiness of foot varies somewhat with the species, but in *D. spectabilis* hair occurs upon the toes save upon the terminal pad, and is longest upon the sides, here being fringe-like. The sole is also densely covered with short hairs which are longest near the base of the toes. Upon the dorsal surface of the foot the hairs are white, but sooty upon the plantar surface of this species, although white in *D. deserti*.

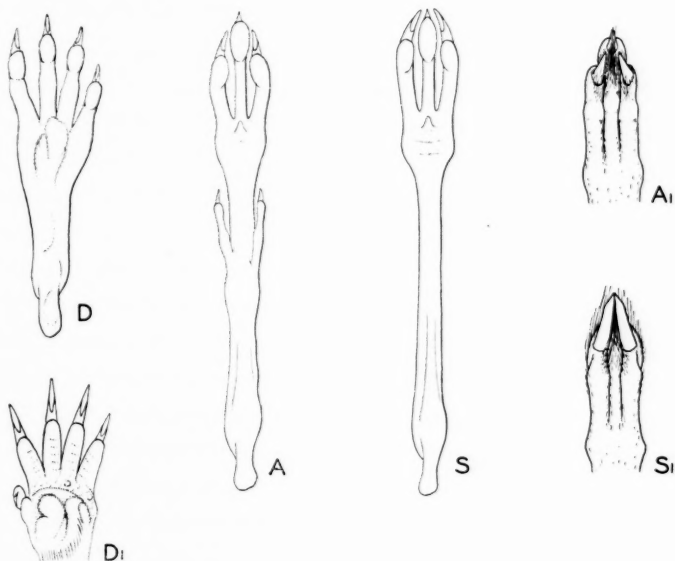


FIGURE 5. Plantar aspect ($\times 1$) of the left pes of *Dipodomys* (D), *Allactaga* (A), and *Scirtopoda* (S). Palmar aspect ($\times 2$) of the left fore foot of *Dipodomys* (D₁). Dorsum of the distal pes of *Allactaga* (A₁) and *Scirtopoda* (S₁), showing characteristic central inclination of nails.

In the jerboas the hind foot, as well as the shank, is greatly elongated. The middle toe without claw is about 23 per cent of the total foot length, so the toes have experienced approximately equal elongation with the foot as a whole. The number of digits is variable,

but there are always three terminal digits,—the second, third, and fourth. These may be all that are externally present, as in *Dipus* and *Scirtopoda*, the first and fifth may be retained farther back on the pes, as *Allactaga* and *Euchoreutes*, or the first may have disappeared and the fifth retained in a reduced state, this condition being solely represented by the genus *Scarturus*.

In *Dipodomys* there is a tendency for the terminal part of the second and fourth digits to slope toward the third, as discussed more fully elsewhere, and in *Scirtopoda* this is carried to an extreme. In preserved specimens of the latter, as undoubtedly in life, the tip of the second claw touches that of the fourth, these being relatively on a line with the digital axis. The much shorter and smaller claw of the third digit, however, is almost at a right angle to its first and second phalanges, and with the other two claws, it therefore points upward between the other two. All the digits in this animal would therefore seem normally to be used fairly closely adpressed and as a single complex. It therefore seems indicated that the toes of the jerboas are not spread fanwise to function on soft sand like a snowshoe, but are held together to act as a single digital detail. In the preserved specimens they are maintained at a fair right angle with the metatarsus, irrespective of whether the latter be flexed or extended in regard to the shank, being held in this position by the tone of the flexor fibularis tendons.

The terminal digital pads are not broad but are very deep indeed and are definitely creased. With the toes adpressed the middle pad is somewhat in advance of the other two, and the middle digit is considerably the slenderest. In figure 5 the foot is illustrated as without hair, to show detail, but actually the sides of the toes are very densely fringed with long, sooty hairs (see frontispiece). These do not hide the terminal pads of digits 2 and 4, but they do cover that of 3. This long hair also covers the metatarsophalangeal expansion of the foot and becomes progressively more scanty and shorter proximally. Over most of the metatarsus the hairs are most dense along the depression, clearly visible, between the flexor tendons and the bone. The tarsal prominence and the heel are naked. There is but one plantar pad or tubercle, high and pointed and set well back from the base of digit 3.

Although the middle three digits of *Allactaga* superficially resemble those of *Scirtopoda* because of the elongation of the foot, basically they are somewhat different. The second and fourth nails also slope toward the third, but the latter is not elevated to a right angle with

its phalanges, nor do the second and fourth nails approach one another to the point of contact, for the third digit interposes. The nails are also shorter than in *Scirtopoda*. The terminal pad of the third toe is very broad and flat, while those of the second and fourth, although equally as extensive in a vertical direction are rather narrow where they touch the ground, and fit back of, and to either side of, that of 3. The borders of the digits and of the foot are lightly fringed with rather long hairs, but not to anywhere near the extent as in *Scirtopoda*. The single plantar tubercle is larger than in that animal and situated farther forward. The first and fifth digits are very much more slender than the others and the first is slightly shorter than the fifth. Their positions upon the foot are better illustrated than described. The metatarsal area of the sole is naked, indicating, I should think, more frequent contact with the ground than in *Scirtopoda*.

Excessive hairiness of the digital area appears to be characteristic of the 3-toed jerboas, but not of those having four or five digits. The foot of *Euchorcutes* is essentially like that of *Allactaga*, except that in the former the terminal digital pads are phenomenally developed, and this is also the case with the 4-toed *Scarturus* save that the hallux is lacking. The foot of *Pedetes* is on the general plan of that of *Dipodomys*, although somewhat more specialized.

In a fresh specimen of *Dipodomys* (*D. agilis*) examined soon after death and manipulated so as to overcome the effects of rigor mortis it was found that the greatest angle which the thigh could assume with respect to the vertebral axis was about 135 degrees, but it is doubtful whether so extreme a position (in a posterior direction) can be attained voluntarily. In normal static posture the thigh-vertebral angle approximates zero; or in other words, the femur is then virtually parallel with the body axis.

Maximum extension of the shank with respect to the thigh was about 135 degrees, so that it is not quite possible for the animal to hold these two segments in a straight line. In fact it is doubtful whether in practice this angle exceeds 120.

In shank-thigh flexion there was only a slight amount of tonal flexion of the pes—to about 120 degrees—which can probably easily be overcome by antagonistic muscular effort. In shank-thigh extension there was strong inhibition of foot extension, the shank-foot angle remaining at practically 180 degrees, and the latter was the greatest amount of flexion of which the foot is capable.

At the heel there was no discernible pronation or supination, but because of the long foot and the looseness of its ligaments movement

of the toes was possible for about 75 degrees in either direction. The corresponding figures for *Neotoma* were 100 degrees in supination and 75 in pronation. When the leg was flexed there was gradual involuntary flexure of the toes, undoubtedly through the action of the deep flexor tendons, until at the maximum of this action the foot-toe angle was about 135 degrees.

Unfortunately there has been no opportunity to examine a fresh specimen of jerboa so as to study the limb action, and preserved specimens are entirely untrustworthy for this feature. On the whole the flexor-extensor action of the limb segments is probably not greatly different from that of *Dipodomys*, save that there appears to be a greater amount of automatic flexion of the toes of *Scirtopoda* when the pes is sharply extended with respect to the shank. In the more specialized jerboas, such as those dissected, there is probably also some reduction in the rotational action of the segments, especially of the pes, in which there should be possible very little supination and pronation.

MYOLOGY.

The material, representing saltatorial rodents, which was dissected in the present connection comprised a number of individuals of *Dipodomys spectabilis*, two of *Scirtopoda orientalis*, and two of *Allactaga mongolica longior*. Not all of the *Dipodomys* were completely dissected, only particular points of some of the specimens having been investigated. The condition of these was excellent, as was that of the *Allactaga*, save that both of the latter had been caught in traps and some of the muscles of the thorax quite severely damaged. In addition these and the specimens of *Scirtopoda* had become hardened in a flexed position so that some difficulty was experienced in investigating small muscles of the subcervical and other regions. This was especially pronounced in *Scirtopoda*, the muscles of which had been bleached and rendered especially tender by years in alcohol, so that they were very prone to tearing. While dissecting all of these certain details of the genus *Zapus* were also examined.

In connection with the myology it should again be mentioned that the affinity of the jerboas is more nearly with hystricomorphine, and of *Dipodomys* rather with the sciuromorphic rodents, and in consequence many of the differences are attributable to phylogenetic rather than adaptational considerations. This also applies to the wood rat, *Neotoma*, a myomorphine representative, details of which are mentioned from time to time.

A word of explanation anent the designation of muscle groups as flexors or extensors may here be in order as investigators, including myself, have frequently neglected properly to indicate the nomenclature which they have intended to follow. In the case of a typical quadruped it is certainly more convenient, from a functional viewpoint, to look upon the forward movement of the knee as flexion of the thigh, corresponding to backward movement of the elbow, and this action has been so treated in my previous reports. But this treatment leads to confusion when the phylogeny of the muscle groups is also being considered and is technically incorrect for the reason that all the dorsal muscles of the limbs, including triceps brachii and quadriceps femoris, are extensors of the limbs in the primitive tetrapod posture. This system of terminology is the one that will be followed in the present instance.

The innervation is given for all muscles of *Dipodomys*. No attempt was made, however, to determine the exact number of nerve components serving such segmental groups as the abdominal muscles and sacrospinalis. Furthermore it was found so exceedingly difficult to work advantageously within the reduced space between the shoulder and the greatly inflated bulla that the finer details of the cervico-brachial plexus are not offered. Because of the limited amount of jerboa material available the innervation within this group was sought only in the case of those muscles presenting some particular problem.

Perhaps no plan of arrangement of the muscle system will ever be entirely satisfactory from every viewpoint, and this certainly cannot be the case at present when so much remains to be done on the morphology of muscles. I have found the plan followed in reporting upon the anatomy of the wood rat to be convenient and reasonably satisfactory. Nevertheless it is somewhat deficient from the morphological aspect and accordingly I have herewith adopted a system of muscle arrangement that is essentially phylogenetic in character, based, for the most part, on tenets that are reasonably well known and established. Some compromises, however, have been necessary, as in separating, under extrinsic and intrinsic muscles of the shoulder, the latissimus dorsi and teres major, which are components of a common group. Such a system will not be found as convenient for the student who is not thoroughly versed in myology as one more purely topographical in character, for he may not see anything to be gained by dividing groups which he has been wont to consider as closely related, such as the dorsal scalene from the two other scaleni divisions,

but this is the fault of nomenclature that is firmly entrenched—not of the phylogenetic arrangement employed.

The system herewith followed may be briefly presented as follows:

Branchiomic Musculature.

Trigeminal Field (N. V).

Facial Field (N. VII).

Glossopharyngeal Field (N. IX).

Vago-accessory Field (Nn. X, XI).

Myotomic Musculature.

Axial.

Ocular.

Dorsal.

Ventral.

Infero-lateral.

Superior (Hypaxial).

Appendicular.

I. BRANCHIOMERIC MUSCULATURE.

A. TRIGEMINAL FIELD (N. V).

The Mm. tensor tympani and tensor veli palatini were not investigated.

MASTICATORY GROUP.

M. masseter. In the two groups, represented by the jerboas on the one hand and *Dipodomys* on the other, the masseter muscle, with accompanying bony conformation of the skull, constitutes one of the best criteria for supergeneric groupings. Hence, as might be inferred, the masseter muscles of the two groups are basically different.

In both, as in all rodents, I believe, there is a typical masseter superficialis, distinct and largely triangular. In *Dipodomys* the apical half was tendinous and arose from a slight prominence at the premaxillary-maxillary suture between the infraorbital and incisive foramina. Insertion was along the caudal border of the expanded angular process of the mandible, not, however, extending quite to the dorsal tip of the process. In *Scirtopoda* the tendinous part was more restricted and it further differed in that origin was also fleshy, the whole being from the inferior border of the maxillary portion of the zygomatic arch. It thus probably included some of the masseter major components as found separable in *Dipodomys*. Insertion was

upon both outer and inner borders of the angular process and dorsalward to include the accessory process between the angle and the condyle of the mandible. In *Allactaga* origin was even more extensive, to include half or more of the ventral border of the jugal.

In *Dipodomys* the masseter major was robust and arose from the whole rostral surface of the infraorbital lamina of the maxilla and as far rostrally as above the infraorbital foramen. It was inserted, in common with the deep division, upon a characteristic groove upon the mandible, below and parallel with the dental arch. Posteriorly its deep fibers merged with those of the deep division. In the jerboas the masseter major did not occur as a separable muscle.

In reporting on the wood rat I designated the caudal division of the masseter as the masseter zygomaticus, which I now discard as less desirable than the term masseter posterior. In *Dipodomys* this was very well developed and arose chiefly from the posterior part of the zygomatic process of the maxilla, but also from the jugal. Insertion was upon both lateral and medial surfaces of the superior angular process. In the jerboas origin was continuous with and inseparable from that of the superficial division. Insertion, however, was distinct, in *Scirtopoda* upon the dorsal part of the accessory angular process and in *Allactaga* upon the well defined prominence formed below the condyle by the projection of the incisor root; thence, in both animals, for a short distance anteriorly.

The masseter profundus in *Dipodomys* arose from the entire orbital surface of the maxilla and had a broadly tendinous insertion upon the mandible in company with the masseter major. In the jerboas the division was intricate and especially posteriorly its relationship with contiguous divisions was very intimate. It has evidently developed to subserve the same functions as the masseter major in myomorph rodents, which it has been able to do by extending anteriorly through the large infraorbital aperture of the maxilla, and it accordingly arose as shown (fig. 6), as well as from the orbital surface of the maxilla and adjacent jugal. Insertion was as in *Dipodomys* but less extensive.

M. temporalis. This muscle was very much reduced in all three animals. In *Dipodomys* it was double, the dorsal division arising from most of the squamosal, including its process directed toward the meatus, and inserting upon both aspects of the mandibular coronoid process. The deeper, more ventral division arose from the ventral aspect of the squamosal laterally adjacent to the glenoid cavity, and inserted posterior to the coronoid process. In the jerboas

the muscle was single and even weaker, comparable to the dorsal division in *Dipodomys*.

M. pterygoideus externus. This was quite strong in *Dipodomys* but smaller than the internus. Origin was from the lateral surface of the parapterygoid plate with insertion upon the medial condylar process of the mandible. The muscle was smaller in the jerboas.

M. pterygoideus internus. In *Dipodomys* this was very large, origin being from the parapterygoid fossa as usual, and insertion upon the inner, or rather anterior, surface of the extensive angular plate of the mandible. In *Allactaga* it was almost as large but insertion was necessarily less extensive, following the conformation of the mandible. A part of the muscle ended over the entire angular vacuity, so it inserted directly upon the fascia covering this part of the masseter. In *Scirtopoda* it was considerably smaller.

INFERIOR ALVEOLAR GROUP.

M. digastricus anterior. In all specimens the anterior belly of the digastric was distinct from the posterior, but the plan was different in the two groups. In *Dipodomys* the anterior belly, well separated from the midline in its posterior part, arose from the divisional tendon and inserted upon the mandible near the symphysis menti. It was thus not essentially of the sciuromorphic type, as mentioned by Parsons (1894). On the other hand, that of the jerboas was, although in this feature the latter did not conform to what the latter author termed the hystricomorphic type. In the jerboas the digastric tendon formed a tendinous arch over the hyoid and was partly attached thereto. In *Scirtopoda* the anterior belly arose from half this tendinous arch and passed rostrally in contact with its antimeres throughout its length. In *Allactaga*, however, a very odd condition obtained. The fibers that reached the mandible arose from the lateral part of the arch, converging toward the symphysis, while the fibers from the more medial part of the arch inserted upon a midline raphe, and the part of the digastric so inserting seemed to be separable from the remainder. That the latter has nothing to do with the mylohyoid is shown by the presence between the latter and the digastricus anterior of the transversus mandibularis.

M. transversus mandibularis. This was present in all, best developed in *Allactaga* and least so in *Dipodomys*.

M. mylohyoideus. In all three animals attachment was partly to the hyoid, as well as to the medial raphe. The latter part in *Dipodomys* extended but two-thirds the distance from the hyoid to

the symphysis, half the distance in *Scirtopoda*, and one-quarter of the distance in *Allactaga*, in which the muscle was much reduced in area.

FACIAL FIELD (N. VII).

Superficial Group.

Although there has been some dissension with regard to the platysma, I believe that work on the facial field within recent years by Ruge, Huber et al shows conclusively that all of the superficial musculature that is served by the facial nerve has been derived from the primitive sphincter colli of the lower vertebrates. In mammals this has differentiated into three layers, comprising a sphincter colli superficialis, often entirely lacking in the less primitive sorts, a platysma layer, and a sphincter colli profundus. Remnants of the sphincter colli primitivus may occur over the neck. According to Huber the superficial sheet has not led to the formation of any specialized divisions, while the other two have done so, the derivatives often being of extreme complexity and secondarily having migrated over or under other slips in a very intricate manner. It is only by interpreting such slips by means of a generalized ground plan common to many unspecialized mammals that they may be satisfactorily homologized.

The facial musculature of *Scirtopoda* and *Allactaga* is much the same and of a rather simple pattern, so that they may be discussed together. That of *Dipodomys*, however, is so exceedingly intricate, because of the specialization necessary as the external cheek pouches developed, that it must be accorded separate discussion. In four specimens of the latter in which the superficial musculature was dissected there was considerable variation in the definition of individual slips, certain of them being thinner in one specimen than another, or with definable fibers extending farther. Furthermore, the pouch is so extensible in all directions that in one specimen a slip of its controlling musculature may be narrow and in another stretched much more broadly, this depending upon the position in which the pouch was fixed by the preservative, and whether it was empty or distended with food.

In terminology and plan of treatment for this group of muscles I follow Ernst Huber. The jerboas are discussed first, as in them the conditions are so much simpler than in heteromyids.

Scirtopoda and *Allactaga*.

M. sphincter colli superficialis. In *Scirtopoda* this sheet was represented by extremely tenuous fibers over a limited area below the ear (fig. 6), but it was not distinguished in *Allactaga*.

M. platysma. In *Scirtopoda* the platysma proper arose at the midline partly deep to the retro-auricular musculature and, expanding slightly between the superficial sphincter colli and the sterno-auricularis, divided into two slender but well defined slips, one of which extended to the angle of the mouth where it ended superficially to the orbicularis oris, and the other more ventrally to the chin. Its dorsal border was in contact with the auriculolabialis where careful dissection was necessary to separate the two. In *Allactaga* the plan was essentially the same, save that the dorsal border did not extend quite to the auriculolabialis.

In *Scirtopoda* the retro-auricular musculature, consisting of a postauriculo-occipitalis complex, occurred in two layers. The more superficial of these entirely covered the deeper and extended quite broadly from the midline to the base of the ear. The second layer was also broad, but thinner, with fibers running more strictly laterally to the base of the ear. In *Allactaga* there were also two layers. The superficial was about as in *Scirtopoda* but heavier, while the deeper, extending farther ventrally and therefore visible from beneath the posterior border of the superficial layer, extended to the cartilage of the ear in three tenuous slips.

In both jerboas the mandibulo-auricularis was narrow but robust, extending from the auricular cartilage to the posterior border of the mandible just ventral to the condyle.

M. sphincter colli profundus. All except the specialized parts of this sheet were lacking. Posteriorly in both genera there was a slender sterno-auricularis, extending from the ear cartilage, beneath the platysma, and quite to the sternum, attachment being about at the first sternite rather than clearly to the manubrium. The more ventral part of this slip is of course homologous to the sterno-fascialis, where this occurs alone as in *Neotoma*. In both animals the auriculolabialis extended from the ear cartilage, below and in close relation with the orbicularis oculi, and deep to the superior branch of the platysma and the orbicularis oris. Above its origin was a reduced frontalis, a mere remnant in *Scirtopoda* but larger in *Allactaga* and extending as far as above the eye. There was also a very small interscutularis in both, extending but a short distance

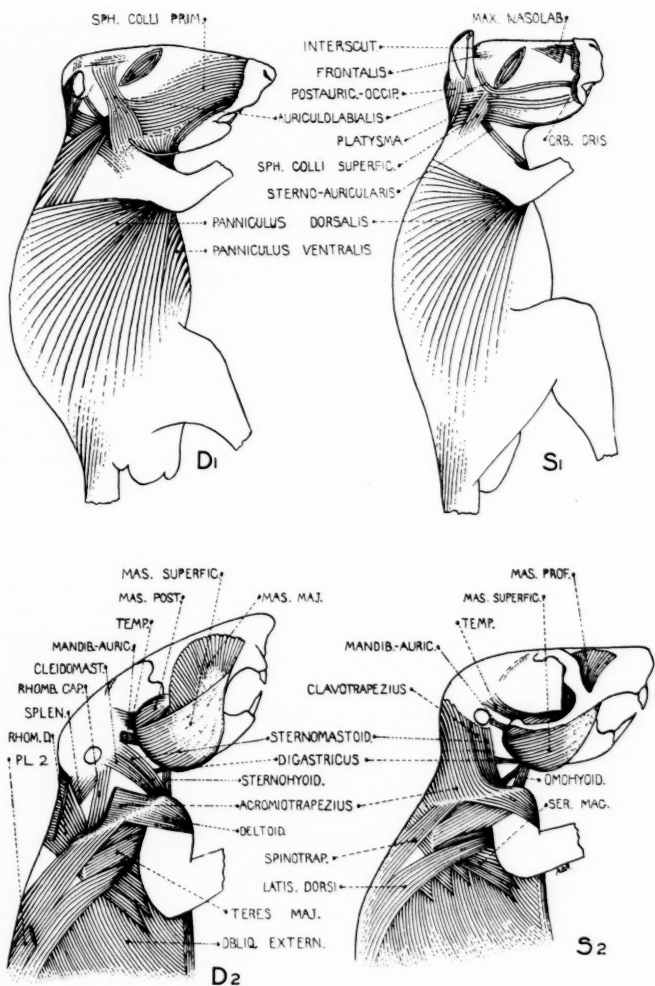


FIGURE 6. Superficial cutaneous (facial and panniculus) musculature of *Dipodomys* (D₁) and *Scirtopoda* (S₁), above. Below, the superficial musculature of the shoulder and masticatory musculature of the same genera (D₂ and S₂).

from the ear. In both, also, the nasolabialis was about as usual in rodents and was simply triangular. Deep to this, but partially visible along its superior border, was the maxillonasolabialis. In *Scirtopoda* this took the form of a slender pars nasalis, and a short and equally slender pars labialis (fig. 6) extending beneath the more posterior of the vibrissae follicles, these being larger than the remainder of the follicles. In *Allactaga* the pars nasalis occurred in two divisions. The deeper was largely like the single slip in *Scirtopoda*, while the superficial arose in two slender parts, these then joining and sending a thread-like tendon which broadened over the dorsal part of the nose. The pars labialis was as in *Scirtopoda* save that it slanted more toward the nose than the lip.

The orbicularis oris is indicated in the drawings but all of its fibers were not followed with exactitude. The buccinatorius was as usual in rodents, being more extensive in *Allactaga* as an accompaniment of the relatively longer rostrum. It was a rather simple sheet in both, and its indicated ability to act as an oral sphincter was not considered to be more marked than in the wood rat.

Dipodomys.

There was no indication of any sphincter colli superficialis. The muscles present were exceedingly involved and curious, departing widely in their development from the fundamental arrangement, undoubtedly because of the requirements of the external cheek pouches. The control of the latter is intricate, for the muscles must act largely in groups.

M. sphincter colli primitivus. From this has developed the superficial sheet of muscle covering the pouch. It took origin from the midline chiefly deep to the postauriculo-occipitalis complex and passed deep to the two divisions of the platysma. A part, indicating its homology, then extended for a short distance over the shoulder before disappearing, but the main portion had secondarily invaded the side of the head to the mystacial pad. After passing deep to the platysma it expanded, as suggested in fig. 6, its relationship with the labial extension of the auriculolabialis being so intimate that the two could not be readily separated. Although it closely approached the orbicularis sacculi and the fibers were parallel, the latter was not derived from this sheet.

M. platysma. The platysma proper usually occurred dorsally over the shoulder in two slips. The more superficial arose from the fascia near the midline, in the same layer with, and almost joining,

the panniculus. Above the posterior extremity of the pouch it disappeared beneath the ventral extension of the auriculolabialis. It there divided into three portions. The part (*a*) was the more superficial and extended to the dorsolateral part of the pouch as shown (fig. 7, D1), but stopped considerably short of the orbicularis sacculi. Entally a somewhat similar part (*b*) went deep to the pouch and inserted upon the middle half of its ental surface (fig. 7, D2). A third part (*c*) split off and in the form of a slender slip passed deep to the posterior termination of the pouch, emerged from its ventral border so that it could pass superficial to the caudal border of the gular sheet of the sphincter colli profundus (fig. 7, D1 and D4), and so extended to the chin.

The part of the platysma which is termed for convenience the deeper division arose from the fascia near the midline in a position which covered the anterior half of the latissimus dorsi origin—therefore deep to the panniculus. It emerged from the latter only to pass beneath the superficial division of the platysma, extending narrowly and partially deep to the dorsal border of the pouch and then expanding to insert upon the anterior part of its ental surface, medial to slip (*b*) of the superficial division. In another specimen the origins of platysma 1 and 2 were practically continuous and the second division did not separate until it dipped beneath the first, posterior to the auriculolabialis. In addition the first division covered the entire pouch.

The three divisions of platysma 1 are really not so surprising. It is clear that they separated from the primitive platysma sheet as the pouch developed, the latter obliging slip (*c*) to adopt an unusual expedient. The origin of platysma 2 has migrated rearward beneath the panniculus, but its path of development as it finally has passed beneath platysma 1 is less apparent.

In *Dipodomys* the postauriculo-occipitalis complex occurred in three layers (fig. 7, D3). The most superficial of these was a broad, thin, triangular sheet arising from the midline and inserting along the occiput to the craniomedial base of the ear. The second was an extremely tenuous slip, also from the midline and passing to the medial part of the bulla. The third extended to the base of the ear, where it inserted by two slips as shown. The mandibulo-auricularis arose from the auricular cartilage and inserted upon the medial aspect of the superior angular process of the mandible.

M. sphincter colli profundus. At the medial base of the ear there was a small remnant of the interscutularis that did not reach even

half way to the midline; and rostrally, a better defined frontalis, extending somewhat over the eye.

In one specimen at least the auriculolabialis certainly was entirely superficial. The original part was well defined and there was nothing noteworthy regarding its anterior fibers, these extending to the snout. Posteriorly, however, the major portion of the muscle had secondarily migrated ventrally, thus covering both the platysma and sphincter colli primitivus, and disappearing over the lower border of the pouch. Over the rostrum there had also been a secondary expansion dorsally, so that fibers as shown (fig. 6, D1) now entirely hide the nasolabialis. This rostral portion is now, apparently, completely fused along its border with the forward extension of the sphincter colli primitivus. In at least one specimen dissected the condition of this muscle was definitely different. The ventral extension covering the sphincter colli primitivus was not so well defined, but there was another tenuous extension beneath the primitivus, and in less intimate relationship with that sheet than with the underlying platysma (division 1), which the connection had pulled dorsally so that the platysma extended superiorly practically to the base of the ear cartilage.

The gular sheet of the sphincter colli profundus also varied individually in its definition. In one specimen it did not extend as far laterocaudally as the pouch. Perhaps usually, however, it is more pronounced, arising from the midline at least as far posteriorly as about the second sternite, and to a point somewhat forward of the ventral border of the external opening of the pouch, but not to the chin. Both posterior and anterior borders of this sheet were heavier, especially the latter, the fibers here passing around the ventral opening of the pouch (fig. 7, D1) to continue dorsorostrally as the orbicularis sacculi, and so to the mystacial pad. Thus, although the orbicularis oris is also a derivative of the sphincter colli profundus it is likely that the latter became differentiated far in advance of the orbicularis sacculi, which was developed from the same layer as the pouch began to form. It is seen that the posterior border of the gular sphincter colli was pulled forward by the third slip of the superficial platysma (fig. 7, D4), and that its dorsal border was indicated (fig. 6, D1) as not quite reaching either the auriculolabialis or the sphincter colli primitivus. Effort was made in several specimens to ascertain whether fibers of one of these layers did not actually pass over or under the other, but they were too slightly differentiated at this point to determine the question.

Deep to all the other facial muscles upon the side of the head was

the usual sterno-auricularis, extending slenderly from the base of the ear to about the first sterneber. The ventral portion was there-

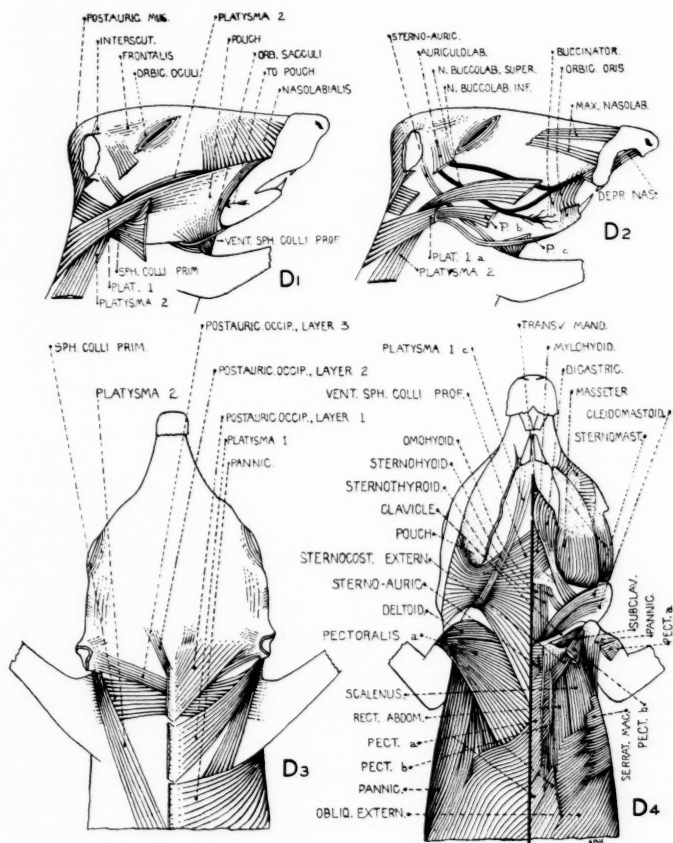


FIGURE 7. The musculature of *Dipodomys*. Details from the lateral aspect of the middle (D₁) and deeper (D₂) layers of the facial muscles; and from the dorsal (D₃) aspect. Ventral (D₄) aspect of the cephalic and thoracic muscles, superficial layer to the left and deeper details to the right of the mid-line.

fore well beneath the gular sheet of the sphincter colli profundus, which is a very interesting occurrence. This slip is also a derivative of the sphincter colli profundus. Therefore it evidently separated from the latter in some ancestral form, the gular sheet then first contracting somewhat, but later extending to cover the ventral part of the sterno-auricularis as specialization of the pouch progressed.

The nasolabialis was not triangular as usual but the insertion, especially, was very extensive (fig. 7, D1), and it undoubtedly has developed for the purpose of aiding in control of the inner margin of the pouch. Beneath it were two small slips of the maxillonasolabialis. The pars nasalis extended to the nose, and the pars labialis, with more ventral origin, diverged to the upper lip.

The orbicularis oris was of the usual pattern and there was not discernible any specialization attributable to the pouch. The buccinatorius was, however, highly specialized. In the kangaroo rats the part of the mouth posterior to the incisors can evidently be much more tightly closed than in most rodents. Whereas in the wood rat there is an oral pad upon either side which the normal tone of the buccinators keeps in contact, thus closing the mouth posterior to the incisors, in *Dipodomys* the more caudal part of the buccinators themselves have differentiated, they being attached to the lower rostrum above and the mandible below, in such fashion that the pair can operate practically as a single, circular sphincter, thus closing the mouth very tightly. The anterior part of the buccinator, however, descends from the side of the rostrum as usual. From the sphincter colli profundus has also developed a small muscle extending dorsally from the anterior base of the upper incisors to the nose; this small muscle may be termed a depressor nasalis, but whether its relationship is closer to the orbicularis oris or buccinatorius is not clear.

Deep Group (of N. VII).

M. stapedius. In *Dipodomys* the muscular process of the stapes was especially poorly defined and the muscle appeared to be correspondingly smaller.

M. stylohyoideus. In *Dipodomys* origin was from the bulla medial to the styloglossus, and in the jerboas from the paroccipital process. Insertion was upon the hyoid as usual.

M. digastricus posterior. In *Dipodomys* origin was from the exoccipital process and fleshy fibers practically ceased at the tendinous division between the posterior and anterior bellies. The whole of

this tendon did not pass to the latter, however, but a part split off medially to form with its antimere a poorly defined arch, with slight attachment to the hyoid. The latter detail was carried farther in the jerboas. In these the origin was from the paroccipital process and the whole of the tendinous division between the bellies formed, with its antimere, the tendinous arch, more firmly attached to the hyoid, and from which the fibers of the anterior belly took origin.

GLOSSOPHARYNGEAL FIELD (N. IX).

The part of the pharyngeal musculature served by this nerve was not dissected.

VAGO-ACCESSORY FIELD (Nn. X, XI).

The pharyngeal and laryngeal musculature innervated by this field was not dissected. In this group might properly be placed the sternomastoid, cleidomastoid and trapezius, for they are partially served by the ramus externus of the accessory nerve, but as they are also supplied by the cervical nerves they are grouped with the lateral set of the cervical, inferolateral, myotomic musculature.

II. MYOTOMIC MUSCULATURE.

1. AXIAL MUSCLES.

A. *The muscles of the ocular division* (Nn. III, IV and VI) were not investigated.

B. *Intrinsic dorsal division.*

The long back musculature might here be dismissed with a short description and the statement that it had the usual attachments. Discretion would dictate such a course, for when great specialization of this system is encountered it is extremely difficult to homologize the divisions with those of man, perhaps partly for the reason that certain portions are not homologous with anything in human anatomy but only analogous. Considering that there is a deal of uncertainty regarding the homology of the vertebral processes in mammals and that the erector spinae is now always a single muscle system with parts variously differentiated, this is only to be expected. Nevertheless an attempt will be made toward homologizing the extremely intricate divisions in saltatorial rodents, and these will be discussed at some length.

(a) *Spino-transverso-occipital system.*

In *Dipodomys* the *M. splenius* was extensive, the origin of the posterior part being deep to the serratus posterior superior, while

insertion was over the lambdoidal area to a point caudoventral to the meatus. In *Scirtopoda* it was more extensive along the midline and this was still more pronounced in *Allactaga*. In *Zapus* it did not extend so far caudally as in the others.

(b) Sacro-transverso-transversalis system.

When one encounters two cervical divisions of the erector spinae located lateral to the trachelomastoid, or longissimus capitis, the inner should be considered as of longissimus affinity also, and the outer as a part of the iliocostal.

M. iliocostalis, partes cervicis, dorsi et lumborum. In *Dipodomys* this was greatly reduced in size, although the posterior part had excellent leverage. The pars lumborum arose mostly from the ilial spine, but a few fibers also came from the fascia mediodorsally. As a perfectly distinct, slender muscle the whole passed to an attachment of its fibers upon ribs 12, 11, 10 and 9. Fibers of the pars dorsi, indivisible from the pars lumborum, first arose from rib 11, with increment from each rib farther cranialward. The fiber bundles from each rib were attached to about the seventh rib next cranially, the whole ending in a pars cervicis, which inserted upon the transverse processes of the last four cervical vertebrae.

In *Scirtopoda* the iliocostal was even smaller. In the posterior lumbar region its fibers were inseparable from those of the longissimus, but definition was good behind the thorax. The lumbar fibers inserted upon the last five ribs and from these pars dorsi took origin. In the middle of the thorax the muscle narrowed so as almost to disappear, but became better defined anteriorly, and insertion was upon the transverse complex of the fused cervical vertebrae. In *Allactaga* it was determined that fibers of the iliocostal arose not from the ilium but clearly from the superficial aponeurosis of the longissimus, and that none extended farther to the rear than the middle of the lumbar region. This may really have been the case in *Scirtopoda* also, a point impossible of determination because of the bleached and fragile condition of the fibers. Insertion was as far forward as the third cervical.

The inner part of the sacro-transverso-transversalis system in reality consisted of two distinct divisions, a lateralis comprising that part of the usual longissimus that attaches to the costae, and a medialis that ordinarily has more medial attachments. These for convenience will accordingly be considered as two muscles.

M. longissimus lateralis, partes capitis, cervicis, dorsi, lumborum (et caudalis?). It is not at all improbable that a part of the extensor

caudae lateralis as found is homologous with the longissimus lateralis, but this is not certain and for convenience it will be discussed with the medial division. In this connection it should be stated that the homology of the caudal muscles of long-tailed mammals has received so little attention that disposition of the caudal components in any phylogenetic scheme can be only tentative.

In *Dipodomys* pars lumborum of the lateral longissimus was extraordinarily robust. Its fibers arose partly from the medial surface of the ilium (but not from the sacrum) and from the dorsal fascia. From the ectal surface of the latter the more lateral fibers originated, and from the ental surface the deeper ones; and in the lumbar region all fibers curved laterocranially around the loin in a heavy, semi-cylindrical mass to insert upon the ventral surface of the anapophyses of the last two thoracic and first four lumbar vertebrae. As the curvature of the fibers was such that those caudally inserted no farther back than the fourth lumbar, well defined anapophyses were lacking upon the last three lumbar. All but the last two thoracics were also lacking in sharp anapophyses, and here the pars dorsi was accordingly of a different character. Its posterior, superficial fibers continued from the dorsal fascia but origin of the remainder was by small tendons, apparently from the dorsal metapophyses, with insertion upon the ribs considerably farther forward. The whole continued uninterrupted into the pars cervicis, with tendinous attachment to the transverse processes of the last six cervicals. Pars capitis, constituting a trachelomastoid, was entirely separate. It seemed not to have attachment to any of the cervical vertebrae but arose from the first eight thoracics (metapophyses?) and inserted upon the audital bullae caudoventrally to the meatus.

In *Scirtopoda* the pars lumborum was basically similar to, but of little more than half the width of, that of *Dipodomys*. The pars dorsi, however, was broader, and anterior attachment was upon the transverse cervical complex medial to the iliocostalis. In robustness this division in *Allactaga* was intermediate between conditions in the other two, with attachment to the last four cervicals. Accompanying the lesser size of this muscle in the jerboas the lumbar anapophyses were shorter, especially in *Allactaga*, than in *Dipodomys*.

Whereas in *Dipodomys* the cervical part of this division was definitely associated with pars dorsi and inseparable from it, in the jerboas the pars cervicis was rather associated with the trachelomastoid, constituting to all intents a shorter, cervical division of the latter. In *Scirtopoda* it arose from thoracics 4, 3 and 2, and inserted

upon not only the transverse complex of the last six cervicals but upon the atlas as well. In *Allactaga* it arose from the first four thoracics as well as the posterior cervicals, and inserted upon the atlas. Pars capitis—the trachelomastoid—arose in *Scirtopoda* from thoracics 8, 7, 6, 5 and possibly 4, and inserted upon the caudal border of the meatus just deep to the sternomastoid, while in *Allactaga* conditions were the same save that insertion extended farther dorsally.

M. longissimus medialis should be treated as of the trunk and of the tail. Part of the caudal division, or extensor caudae lateralis, certainly belonged with the longissimus medialis, and perhaps all of it did. At any rate, as an accompaniment of the extreme specialization of the longissimus the fleshy part of the lateral extensor of the tail was perfectly divisible into three portions, which may be termed ectalis, intermedius and entalis (fig. 8, D2). In *Dipodomys* pars ectalis arose from the caudal aspect of the ilial aponeurosis and from the sacral transverse processes, and a single tendon extended from it upon the lateral side of the tail; so its functions are as much those of an abductor as an extensor. The pars intermedius had the same origin as the pars ectalis but farther forward, and the two were separated by a deep fascia. At the base of the tail this part was entirely deep to the ectalis but its three long, caudal tendons occurred upon both sides of that of the ectalis. It also sent shorter, deeper tendons to insert upon the metapophyses of the first few caudal vertebrae. Pars entalis was really nothing but a caudal continuation, by a single long tendon, of the middle division of the longissimus medialis, although shorter tendons from this muscle also inserted deep upon the basal caudal vertebrae. One gained the impression that upon contraction of this division of the longissimus farther forward the tail would be extended automatically, unless controlled by antagonistic action of the caudal flexors.

In the jerboas a largely similar condition prevailed, save that some of the fibers of the pars intermedius were in direct continuation of the longissimus lateralis, especially in *Scirtopoda*, and that in the latter the pars entalis sent four long tendons along the tail, while in *Allactaga* this was at first a robust, single tendon which later split into four branches.

The part of the longissimus medialis occurring upon the body proper of *Dipodomys* was also divisible into three parts, more distinct transversely than axially. These may be termed anterior, intermediate and posterior divisions. The anterior of these was really the most superficial (although all were mostly hidden by the longissimus

lateralis) and its fibers took origin from the lateral side of the tendons of the semispinalis dorsi, which arose from the metapophyses of the first five lumbar. The fibers inserted upon the articular processes of the last four thoracics. Next, the posterior division arose from the aponeurosis attached to the superior border of the ilium. The fibers twisted around mostly deep to the intermediate division to insert upon the anapophyses of the first five lumbar and last two thoracics. Finally, the intermediate division arose under cover of the semispinalis lumborum from the sacrum and the tendons of the extensor caudae lateralis and also inserted, but dorsal to the posterior division, upon the anapophyses of the first five lumbar and possibly the last thoracic as well.

In the jerboas the medial longissimus was single and its fibers were distinct from those of the lateral division only in the superficial part of the muscle. It arose from the medial ilium and the dorsal aspect of the sacrum, and inserted upon the anapophyses of the last two thoracics and first four or five lumbar.

(c) Spino-spinalis system.

M. spinalis. In *Dipodomys* this system seemed to be entirely absent, although there may have been a few of its fibers present between the spines of the last thoracic and fourth sacral vertebrae. In *Scirtopoda* it was definitely present between these spines and in one specimen attachment was to the first caudal as well as the last sacral. In *Allactaga* what appeared to be a homologous slip occurred stretching forward from the last sacral spine, but it did not reach as far as the last lumbar, the fibers ceasing abruptly upon a medial aponeurosis.

(d) Transverso-spinalis system.

In many mammals, apparently, the relationship of the fibers constituting the semispinalis, multifidus and submultifidus (or rotatores) elements of this system is extremely close, so that no clear separation is practicable and one is uncertain of the proper term to use for some component that occurs. But after all it is largely an academic question whether the term semispinalis is employed, the fibers of which may pass over more than four vertebral spaces, or multifidus, which may pass over three. In my study of the wood rat the extensor caudae medialis appeared to continue directly forward into the lumbar region, and as this caudal muscle is conventionally believed to be of multifidus affinity I accordingly called the lumbar part by this name. In the rodents now under discussion, however, these two parts appear to be largely distinct. I am now reasonably

certain that the lumbar part of this system in these mammals, and the wood rat as well, has fibers that are too long to be with propriety termed multifidus, while this objection does not hold for the caudal part. Suffice it to say, however, that the semispinalis lumborum, so termed, and the extensor caudae medialis in the rodents discussed, have both been derived from the transverso-spinalis system.

M. extensor caudae medialis took origin in all three genera from the first and subsequent caudal spines, insertion of each bundle then being upon the metapophyses of the third vertebrae next to the rear. The bundles rapidly became smaller and their insertions more tendinous.

M. semispinalis. The division which appeared to be representative of this group was composed of partes capitis, cervicis, dorsi et lumborum. In *Dipodomys* it was very broad and was largely superficial by virtue of the fact that the spinalis system was practically absent and the longissimus situated more laterally. Pars lumborum arose from the aponeurosis that extended from the ilium over the extensor caudae lateralis, and inserted upon the spines of all the lumbar and last three thoracic vertebrae, possibly with the exception of the last lumbar. Pars dorsi adjoined but was not strictly continuous with the last. Origin was chiefly by tendons from the metapophyses of the first four lumbar and last two thoracics. The fibers passed over several vertebral spaces and at the midline were tucked in to insert deep upon the short spines of the anterior thoracics, except that a number of the more lateral fibers, indivisible from the rest farther backward, separated and passed as a narrow slip superficial to the remainder in a medial direction (fig. 8, D2) to insert upon the ligamentum nuchae. There seems no possible course but to consider this as a part of the semispinalis. The pars cervicis, hidden by the pars capitis, was distinct and arose from the first six or seven thoracics and inserted upon the common spine of the fused second and third cervicals. The pars capitis was quite heavy but could not be separated into biventer cervicis and complexus. It arose from the first eleven thoracic vertebrae but apparently not from any cervical, and inserted upon the supra-occipital and just laterally upon the bulla.

In *Scirtopoda* the pars lumborum was smaller and insertion was upon the spines of the second to sixth lumbar. Origin of the pars dorsi did not begin so far to the rear as in *Dipodomys*, but the exact number of vertebrae involved was especially difficult to determine. Insertion was upon the thoracic spines, although there may have been no definite attachment to the first two; but fibers extended over these, nevertheless, to rather weak insertion upon the spinal complex of

the fused cervicals. Pars cervicis took origin from the first five, or possibly six, thoracics and inserted upon the cervical spinal complex. The lateral fibers of the thoracic part of the semispinalis were found to be separable and these, arising from all twelve thoracics, continued on to form a single pars capitis, inserting more broadly than in *Dipodomys* upon the more extensive supra-occipital.

In *Allactaga* pars lumborum was essentially as in *Scirtopoda*, but it is interesting to note that the thoracis mass showed a modified condition of that existing in *Dipodomys*. The lateral fibers occurred in a slip that was distinct throughout its length. The most superficial of these arose from the aponeurotic sheath of the longissimus, but the deeper fibers had origin from the original tendons of the medial longissimus, rather than from the processes direct, over about the last five thoracics, and passed superficially craniomedially over the rest of the muscle to insert upon the nuchal ligament. Because of the position of this nuchal slip, chiefly its original part, it appeared that its relationship in this animal, and therefore inferentially in *Dipodomys*, may really be with the semispinalis capitis rather than the pars dorsi. The remainder of the dorsal semispinalis, mostly deeper, arose from most if not all of the dorsal vertebrae, each bundle passing over several vertebral spaces to insert upon the dorsal spines, possibly to include the last one or two of the cervicals. Pars cervicis was essentially as in *Scirtopoda*. Origin of pars capitis began where origin of the outer slip of the pars dorsi ended and was from the first seven thoracics. The insertion was slightly more extensive upon the supra-occipital than in *Scirtopoda*.

Of the shorter elements of the transverso-spinal system of the trunk proper—multifidus and rotatores—there were, in *Dipodomys*, only the latter clearly defined in the lumbar region, while both occurred in the thorax. In the jerboas both seemed to be lacking in the lumbar region, while with certainty only the rotatores could be detected in the thorax.

(e) Intervertebral system.

Modified intervertebral group. Because of the peculiar occipital conditions in *Dipodomys* the conformation of the deep supracervical musculature was somewhat altered. The obliquus capitis superior extended from the lateral atlas to an extensive area over the caudo-medial aspect of the audital bulla, the obliquus capitis inferior had its usual attachments to axial (plus third cervical) spine and lateral atlas, and probably because of the reduced occipital area the rectus capitis posterior was single, from the axial spine straight dorsally

to the supra-occipital and in contact with its antimer. No distinct rectus lateralis could be demonstrated.

In the jerboas there were well developed major and minor divisions of the rectus capitis superior, and obliqui capitis superior and inferior. In *Scirtopoda* there was a very short rectus lateralis, which was better developed in *Allactaga* with its longer neck.

Of the remaining intervertebral muscles the interspinosi and intertransversarii elements were present in all, the former being especially strong in the lumbar region of the jerboas, possibly in compensation for the lack, or virtual lack, of multifidus and rotatores. It should here be mentioned that only the medial intertransversarii belong with the intrinsic dorsal musculature, the lateral ones having been derived from the ventral divisions of the myotomes.

(f) *M. scalenus posterior*. A perusal of anatomical text books shows with what uncertainty this division of the scaleni is regarded. Ordinarily it is stated, rather hesitatingly, to be served by twigs from the cervical plexus. Ernst Huber has, however, demonstrated to his entire satisfaction that it is innervated only by the posterior rami of the cervical nerves, wherefore it must be grouped with the dorsal, rather than the ventral, division of the axial musculature. Unfortunately, however, it is often the case that the scaleni of some of the lower mammals cannot be homologized, even topographically, exactly with the three divisions of man. Especially in such small, short-necked rodents as are under discussion it is virtually impossible to determine with thorough satisfaction whether or no the scalene complex is served also by branches of the rami posterior, and accordingly, whether or not the homologue of the human scalenus posterior be actually present. For this reason the components of the scaleni will all be discussed together (page 430).

Innervation of the intrinsic dorsal musculature is by short branches of the rami posteriores of the spinal nerves.

C. Ventral division.

A'. Infero-lateral system.

(a). Cervical region.

a'. Lingual set (N. XII).

M. styloglossus. This muscle, superficial to the hyoglossus, was very slender. In *Dipodomys* origin was from the bulla lateral, and in the jerboas dorsal, to the stylohyoid. Insertion was into the tongue as usual.

M. hyoglossus. Origin of this muscle, next deep to the geniohyoid,

extended from the midline laterally upon the hyoid, the fibers diverging laterocranially to the tongue.

M. genioglossus. This was narrow and deep, with fibers parallel to and adjoining the midline. Origin was from the hyoid partly deep to that of the hyoglossus.

The intrinsic lingual musculature was not dissected.

Innervation of the lingual set is by the N. hypoglossus (XII).

b'. Medial set.

M. geniohyoideus. This muscle is immediately beneath the mylohyoid. It was parallel to and adjoined the midline, was rather narrow and stretched as usual from the hyoid to the mandible. Innervation is by a filament from the n. hypoglossus.

M. sternohyoideus. In all three rodents dissected origin of this muscle was not from the manubrium and the first sternal cartilage. On the contrary, presumably because of the shortness of the neck, origin was from the dorsal surface of the first sterneber and slightly from the second costal cartilage of *Dipodomys*, while in the jerboas it had spread far laterally upon the second cartilage. Insertion was as usual upon the hyoid.

M. omohyoideus. This was present in all three but absent in *Zapus*. In *Dipodomys* it was more nearly parallel to the sternohyoid than in the others, and had the usual attachments upon scapula and hyoid.

M. sternothyroideus. The origin of this muscle, fused with the sternohyoid, was from the dorsal surface of the first sterneber, the two separating at about the first rib. Insertion was upon the hyoid as usual.

Innervation of these three muscles is by branches from the ansa hypoglossi.

c'. Lateral set.

Mm. intertransversarii laterales. As already mentioned this part of the intertransversarii belongs with the ventral axial musculature. The bundles were well developed in the lumbar region.

M. scalenus. Although the dorsal scalene, as in man, belongs with the dorsal axial musculature, the whole complex will be described here, for the reason that it is not readily separable, as already explained. In most, if not all, rodents it seems safe to say that the strict homologue of the scalenus anterior of man is absent, for no part of this complex is situated ventral to the brachial plexus and sub-

clavian artery. In *Dipodomys* there was but a single scalene, entirely indivisible anteriorly. Origin was by slips from ribs 2 to 5, those from 4 to 5 being deep to the two slips of the serratus magnus originating from ribs 3 and 4. Insertion was chiefly upon the atlas but there was slight attachment also to the transverse processes of the cervicals, chiefly 3, 4 and 5. The absence of a ventral division agrees with the situation in sciurormorph rodents as stated by Parsons.

In the jerboas there was distinctly a small, ventral scalenus, dorsal to the brachial plexus, which arose from the first rib and inserted upon the cervical transverse processes and upon the lateroventral process of the atlas, better developed than in *Dipodomys*. The larger dorsal division was more comparable to the scalenus of *Dipodomys*, but it arose from ribs 2, 3 and 4, and there was a diminutive deep slip arising from the extreme dorsal part of the first rib, the common insertion being mainly by tendon upon the lateroventral process of the atlas. This deep slip from the first rib might possibly be the homologue of the posterior scalene of man. The only innervation secured for the scaleni was by short branches from the cervicobrachial plexus.

The trapezius and sternocleidomastoid have usually been considered as partly of branchiomic origin, because supplied by the accessory nerve as well as direct branches from the cervical plexus. Addens (1929) has claimed that the ramus externus of the accessory is a modified spinal nerve, but this remains to be proved. These three rodents well illustrate the real homogeneous character of these muscles.

M. sternomastoideus. This arose from the manubrium and possibly from a bit of the clavicle as well. Insertion in *Dipodomys* was upon the bulla below, and in the jerboas behind, the auditory meatus.

M. cleidomastoideus. In *Dipodomys* this muscle, arising from the clavicle immediately lateral to the sternomastoid origin, was about as broad as the latter but slightly deeper. In *Scirtopoda* the homologue of this slip might better be termed a calvotrapezius, but in *Allactaga* there had separated from the latter, toward the insertional end only, a cleidomastoid slip, arising from the clavicle continuously with the acromiotrapezius but soon separating from it in a slender slip and inserting deep to its lateral border behind the meatus. It would be difficult to find three mammals which illustrate to better advantage the theoretical origin of this muscle from the trapezius sheet.

M. trapezius. In *Dipodomys* origin of the spinotrapezius was

fairly continuous with the latissimus dorsi, insertion being upon the dorsal two-fifths of the scapular spine. Origin of the acromiotrapezius extended along the midline as far as the occiput, with insertion along the entire spine to the tip of the acromion. In *Scirtopoda* the spinotrapezius was narrow, inserting upon the dorsal third of the spine. Origin of the acromiotrapezius extended along the midline from just dorsocranial of the spine to the occiput and then laterally upon the bulla dorsocaudal to the meatus. Insertion was as in *Dipodomys*. In addition there was in *Scirtopoda* a clavotrapezius, from the lateral quarter of the clavicle to a point behind the meatus, corresponding in all but position of origin to a normal cleidomastoid, and in reality it might be proper to term it so. In *Allactaga* the spinotrapezius was broad. At origin it was not quite continuous with the acromiotrapezius but the two joined toward insertion and attachment of the whole was to the ventral three-fifths of the spine. Origin of the acromiotrapezius extended laterally upon the skull to a point to the rear of the meatus, as in *Scirtopoda*, but at this point the muscle was fused with the clavotrapezius, the latter splitting off to an attachment upon the lateral clavicle. In *Zapus* the spinotrapezius was excessively slender and long, having attachment to the dorsal half of the spine, and the acromiotrapezius did not extend laterally upon the skull.

(b). Thoracic region.

Mm. intercostales. There was little or nothing distinctive about the intercostals. The externals occurred only between the bony ribs proper and not between the cartilages.

M. sternocostalis externus. The proper allocation of this small slip is problematical, for in small rodents I have found it impossible to determine its nerve supply. It appears, however, to have been derived from the intercostals. In *Dipodomys* it extended in a laterocranial direction from the fascia covering the anterior rectus abdominis to the angle of the first rib. In *Allactaga* it was essentially similar, but it was not detected in *Scirtopoda*. The innervation was not detected, but in a number of other mammals I have found it to be by an intercostal nerve, although some have claimed that it is served by the anterior thoracic.

M. serratus posterior superior. In *Dipodomys* this was narrow, occurring between ribs 5 to 9, origin being partly superficial to the splenius and mostly deep to the serratus magnus. In *Scirtopoda* it was smaller still, occurring between ribs 4 and 7, and in *Allactaga* even more tenuous.

M. serratus posterior inferior. In *Dipodomys* this was relatively heavy, but it was lighter in *Scirtopoda*, and was discernible with clarity in neither *Allactaga* nor *Zapus*. Innervation of both these muscles is by branches of the intercostal nerves.

(c) Abdominal region.

M. rectus abdominis. In *Dipodomys* this muscle was exceedingly broad, especially posterior to the thorax where a lateral slip ended (fig. 8). Origin was from the pelvic bones at the symphysis and there was slight decussation of the two halves, the right muscle here being U-shaped and inclosing the single slip of the left. The muscle was here quite narrow but rapidly broadened and its fibers became inextricably fused over the abdomen with the deeper fibers of the external oblique. Thoracic attachment was to the first rib only. In the jerboas there was no decussation at origin, as there is said often to be in octodonts but not in hystricomorphs. It was almost as broad as, although much less heavy than, in *Dipodomys*, and there was no very marked increase in width over the abdomen, nor was fusion of the fibers with those of the external oblique at all pronounced. Thoracic attachment was also to the first rib only.

All the abdominal muscles were very strong in *Dipodomys* but much weaker in the jerboas.

M. obliquus externus. In *Dipodomys* origin was from the dorsal fascia and by fleshy bundles at the termination of the serrati magnus (anterior) and posterior inferior. Anteriorly insertion was upon the sheath of the rectus, but over the abdomen the midline was practically reached, with fibers running almost sagittally and with the deep ones fused with those of the rectus. Caudally the lateral fibers in a heavier bundle passed lateral to the testis (in the male) and inserted, with the remainder of the fibers, upon the crural arch. Conditions in the jerboas were evidently largely similar, save that there was not such intimate contact with the rectus; but the abdomen of these jerboas was in bad condition and satisfactory dissection could not be accomplished.

M. obliquus internus. In *Dipodomys* origin was from the dorsal fascia slightly more dorsally than the external oblique, and from the crural arch and border of the pubis. Insertion was upon the last three ribs and then upon the transversalis on a line extending from the cartilage of the tenth rib to within about 25 mm. of the symphysis, and thence to the midline. Until well to the rear the ventral part of the muscle was entirely deep to the rectus but near

the symphysis a part split off and passed superficial to the latter muscle to continue as the *M. cremaster*, covering the anterior half of the testis. In *Scirtopoda* this sheet was very thin and tenuous, the fibers hardly reaching the thorax, even dorsally. In *Allactaga* the condition was too poor for dissection.

M. transversus abdominis. Origin in *Dipodomys* was from the dorsal fascia slightly ventral to the internal oblique and from the inner border of the thorax, to the midline deep to the rectus abdominis.

Innervation of the abdominal muscles is by branches of the intercostal, and probably the first lumbar, nerves, not followed in the present instance.

B'. Superior (hypaxial) system.

(a) Cervical region.

M. rectus capitis anterior. As usual this extended from the atlas to the basioccipital and was much smaller in *Scirtopoda* than in the other two genera. No separate rectus capitis lateralis was detected.

M. longus capitis. Origin in *Dipodomys* appeared to be not from the vertebrae but exclusively from the expanded, dorsal portion of the first rib. In *Allactaga* origin seemed to be equally exclusively from the specialized ventral process of the sixth cervical. In *Scirtopoda* the latter process is virtually undeveloped and it was impossible to determine from what precise spot in its immediate vicinity this fragile slip arose. Insertion in all was upon the anterior basi-occipital, this being more restricted in *Scirtopoda*.

M. longus colli. The fibers of this muscle which in *Dipodomys* originated from the ventral process of the sixth cervical inserted upon the medial tubercle of the atlas. The remainder of the muscle arose from as far posteriorly as the fourth or fifth thoracic and inserted upon the cervical vertebrae. This was also the case in *Allactaga*, save that origin did not extend so far caudally upon the thoracic vertebrae; but in *Scirtopoda* the ventral process of the sixth cervical was so lightly developed that marked origin from this point was not apparent. Innervation of both of these divisions is by short branches of the cervical nerves, not sought in the present instance.

(b) Thoracic region—none.

(c) Lumbar region.

M. quadratus lumborum. This muscle occurred between the lumbar diapophyses as usual. In *Dipodomys* posterior attachment was chiefly to a process of the first sacral transverse process, well developed for

this purpose, and to a lesser extent to the part of the ilium adjoining, while in the jerboas most of this connection was with the ilium. In *Dipodomys* diapophyses are virtually lacking upon the first two lumbar and reduced upon the third, while in the jerboas this condition occurs one vertebra farther forward. Accordingly the quadratus here passed over two and three vertebral spaces respectively to attachment upon the last rib. Innervation is by short branches of the lumbar nerves.

(d) Sacro-caudal region.

M. iliocaudalis. This muscle, homologous to a part of the levator ani of man, arose in *Dipodomys* from the medioventral border of the innominate ventrally and slightly cranially of the acetabulum. The fibers passed rearward into 6 tendons which extended upon the lateroventral surface of the tail. Conditions were essentially similar in the jerboas.

M. pubocaudalis. This, corresponding to the lower part of the levator ani in man, arose along the border of the pubis forward of the symphysis and caudally adjoining the iliocaudalis. Insertion was upon the tips of the transverse processes of the first four caudal vertebrae.

M. sacrospinous, undoubtedly representing the combined m. coccygeus and sacrospinous ligament in man, was a short muscle easily overlooked in *Dipodomys* and *Allactaga*, passing from the spine of the ischium (just forward of the obturator notch) to the transverse complex of the sacrum. In *Scirtopoda* it seemed to be represented by the ligament only.

Innervation of these three muscles is apparently by short branches of the pudendal nerve.

Mm. flexores caudae. In the sacral region the caudal flexors were very intricate and they may best be described by treating them as occurring in the usual two divisions, an externus and an internus, and by separating the latter into partes antica, media, et postica. Pars antica was the most superficial of these, arising from the centra of the last lumbar and first sacral vertebrae. Its fibers developed 2 tendons which were the most dorsal of the lower caudal tendons. Pars media was partly deep to the last and arose from the centra of all five sacrals, developing tendons upon its lateral belly. Pars postica was considerably smaller, its fibers arising from the centra of the first two, or possibly three, caudals. The lateral fibers appeared to insert directly upon the third and fourth chevrons, while a tendon

from the medial fibers, adjoining the midventral line of the tail, extended far toward the tip. The flexor externus arose from the ventral surface of all the sacral and first three caudal transverse processes, developing for the most part tendons upon the medial belly, although the posterior fibers inserted directly upon the tendons of the abductor caudae internus. Most of the tendons of all these flexor divisions finally inserted upon the chevron bones.

In the jerboas the fleshy part of these muscles was considerably less robust and more simple. The flexor caudae externus was largely as in *Dipodomys* but in *Scirtopoda* the flexor internus was uniform and indivisible, save as the parallel fibers could easily be forced apart. In *Allactaga*, however, the externus was divisible into two parts, these being anterior and posterior.

The perineal musculature of the sacrocaudal region comprised the following:

M. ischiocavernosus. In *Dipodomys* origin was from almost all of the caudal border of the ischium and forward as far as the symphysis, while insertion was upon the anterior base of the corpus cavernosum penis. Stronger connection with the pelvis was afforded by an elastic ligament from the vicinity of the symphysis to the anterior base of the penis, and another similar ligament posteriorly from the ischial border to the base. In this animal the crura of the corpora cavernosa penis were reduced and not apparent externally as lateral tumefactions. In *Scirtopoda*, however, these corpora were clearly indicated and quite swollen. Evidently as an accompaniment insertion of the ischiocavernosus was more apparently into, rather than on, the penis. Origin was as extensive as in *Dipodomys* but was shifted more dorsalward. Toward insertion the muscle passed beneath a superficial binding ligament that converged from the superficial surface of the crus to the posterior border of the symphysis. In *Allactaga* the corpora cavernosa penis were hardly more marked than in *Dipodomys* but the details of the muscle were more nearly like those of *Scirtopoda*.

M. bulbocavernosus. This was relatively large in *Dipodomys*. Some of its fibers were attached to the posterior ligament described under the ischiocavernosus, and the rest to the surface of the crus; but in the jerboas there was no attachment to the crus save indirectly by a ligament situated mediodorsal to the symphysis.

M. sphincter ani externus was as usual, surrounding the anus.

Innervation of the above three muscles is by branches of the pudendal nerve.

2. APPENDICULAR MUSCULATURE.

A. Pectoral limb.

a. EXTRINSIC SYSTEM.

Dorsal group.

M. latissimus dorsi. Morphologically this muscle should be placed with the *teres major* but for convenience the two are here separated on a topographic basis. In *Dipodomys* it was quite well developed and broad. Origin was from the dorsal fascia fairly continuous with the *spinotrapezius*, while insertion was upon the ventral part of the *teres major* tendon. In *Allactaga* origin was the same, and insertion as in *Sciuripoda*. In the latter animal origin was also continuous with the *spinotrapezius* but the muscle was considerably narrower. Fusion with the *teres major* tendon was not complete so that insertion may more properly be said to have been on the humerus. In *Zapus* the muscle was exceedingly slender. Innervation is by the thoraco-dorsal nerve.

M. rhomboideus. In *Dipodomys* this occurred in two parts. The origin of *pars dorsi* extended upon the midline anteriorly to the occiput, with insertion upon the entire vertebral border of the scapula. *Pars capitis* took origin narrowly from the mastoid region posterior to the meatus, between the *splenius* and the *cleidomastoid*, with insertion upon the anterior two-thirds of the vertebral border of the scapula. In *Sciuripoda* there was but a single rhomboid. Origin extended along the midline to the occiput and thence laterally to a point behind the meatus. Insertion was for a few millimeters along the dorsal portion of the spine and thence along the scapular border to the *glenovertebral* angle. Conditions in *Allactaga* were more comparable to those in *Dipodomys*, for there was a similar *pars dorsi*, and a *pars capitis* with scapular attachment confined to the vertebral border opposite the scapular spine. In *Zapus* there was also a *pars dorsi* and a *pars capitis*. Innervation is by the dorsal scapular nerve.

M. serratus magnus. In *Dipodomys* origin of the posterior part was by five slips, from ribs two to seven, the posterior four of which interdigitated with four slips of the *obliquus externus*, while the anterior two arose from deep slips of the *scalenus*. The main cervical part (*depressor scapulae*) was not separable save by its bundles of origin, which were apparently from the transverse processes of all of the last six cervicals. The *atlantoscapularis superior* might with equal propriety be considered as that part of the *serratus* which arose from the atlas. Insertion of the whole complex was upon

the entire vertebral border of the scapula. In *Scirtopoda* origin did not extend posterior to the fifth rib and insertion continued for a short distance ventrally around the Glenovertebral angle. In *Allactaga* origin included the sixth rib, but the thorax was torn so that some other details were impossible of investigation. In *Zapus* origin included the sixth rib. It will be seen that my observations on *Scirtopoda* do not agree with those of Parsons for the same animal (his *Dipus aegyptius*) for he stated that origin of the serratus extended as far as the eighth rib.

M. atlantoscaphularis superior. This was present in all three animals but, as previously stated, it might just as well be considered as a part of the serratus magnus, for it is merely the separable part of that muscle that arises from the atlas.

M. atlantoscaphularis inferior. This, too, is a derivative of that complex of which the serratus magnus is a unit, but the insertion has migrated distally. Origin was from the atlas as usual and insertion upon the border of the acromiotrapezius and the adjacent part of the clavicle. This was apparently the case in *Scirtopoda* as well, while in *Allactaga* the clavicle was not involved, and accordingly the muscle was situated a bit more dorsally.

Innervation of the above three muscles is by the long thoracic nerve (to most of the serratus magnus) and direct branches from the cervicobrachial plexus.

Ventral group.

M. pectoralis. In *Dipodomys* the pectorals were divisible into four parts at origin and two parts at insertion, and these may be designated as superficial and deep. The former arose in a broad sheet (*a*) from the midline between the manubrial tip and about the last sternum, while the part (*a'*) was narrow and partly deep to the portion (*a*) over the xiphoid. Toward insertion it passed entirely deep to (*a*) and fused with it, the common insertion occupying a restricted area upon the proximal part of the deltoid process of the humerus. The portion (*b*) of the deep pectoral, situated the more anteriorly, was deep to the posterior half of the superficial (*a*), while the deep (*b'*) was, in origin, entirely to the rear of the superficial (*a'*), arising not strictly from the midline but with fibers decussating with those of the obliquus externus and rectus abdominis behind the xiphoid. Toward insertion (*b'*) passed deep to (*b*) and the single attachment was by a slender tendon upon the humeral head.

In the jerboas both superficial and deep pectorals were single,

the former about as extensive as superficial (*a*) in *Dipodomys*, and the latter arising deep to the middle half of the superficial division. In *Zapus* the superficial pectoral was double, as in *Dipodomys*, but the deep pectoral was single, like that of the jerboas except for being very narrow.

In all three animals the scapuloclavicularis was absent, the only part of the sternoscapularis represented being the following:

M. subclavius. In *Dipodomys* this was relatively well developed. It arose from the first costal cartilage and passed dorsal to the clavicle to an attachment that was chiefly tendinous upon the lateral part of that bone. In *Scirtopoda* origin was farther lateral upon the costal cartilage, and still farther in *Allactaga*.

M. panniculus carnosus. There is no justification for considering this sheet as anything but a derivative of the primitive pectoral complex, even where there now occur segregated patches (over the hip of *Pedetes*, et cetera), for innervation of the entire sheet is invariably by the anterior thoracic nerve, the same as for the pectorals. In *Dipodomys* the main part of the panniculus was extensive. Origin of the dorsal part was from the vicinity of the midline, from a point above the axilla to and onto the base of the tail. In the latter situation the sheet was continuous over the midline and was heavier, as I have found to be the usual case in long-tailed rodents. Anterior to the tail base the fibers almost disappeared but became better defined once more over the dorsal part of the abdomen. Insertion of all of this dorsal sheet was upon the proximal part of the deltoid crest near the head of the femur and adjoining insertion of the superficial pectoral. Near insertion, however, the ventral border of the sheet separated to become tucked in deep to the remainder (fig. 6). There was also a ventral panniculus sheet in this animal arising from the midline almost as far forward as the gular sphincter colli profundus and posteriorly to just beyond the level of the groin. Its anterior fibers passed caudodorsally deep to the ventral fibers of the dorsal panniculus, where they soon disappeared over the side, but farther to the rear the fibers were parallel and the two sheets became continuous.

In the jerboas only the dorsal sheet of the panniculus was present and this was very similar to that of *Dipodomys*, also being heavier over the base of the tail.

Innervation of the components of this ventral group is by branches of the anterior thoracic nerve.

b. INTRINSIC SYSTEM.

Muscles of the shoulder.

Dorsal group.

M. supraspinatus. In all three animals origin was from the entire supraspinous fossa with insertion upon the greater tuberosity of the humerus.

M. infraspinatus. Origin was from that part of the infraspinous space not occupied by the teres major. Insertion was upon the lateral part of the greater tuberosity. In the jerboas the origin was

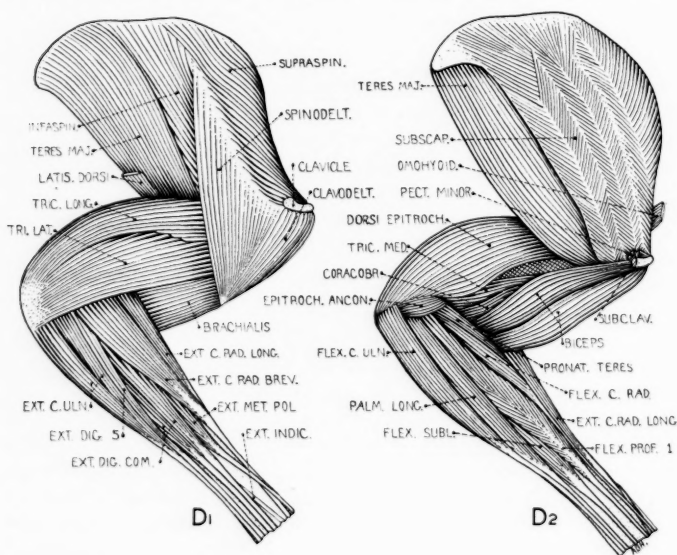


FIGURE 9. Musculature of the anterior limb of *Dipodomys*: lateral (D_1) and medial (D_2) views.

broader relative to the scapular width, therefore actually about the same width in *Scirtopoda* as in *Dipodomys*, and narrower in *Allactaga*. Innervation of these two muscles is by the suprascapular nerve.

M. subscapularis. This muscle was highly multipinnated, with origin from the entire subscapular surface and insertion upon the lesser tuberosity of the humerus.

M. teres major. Morphologically this muscle belongs both with the subscapularis and latissimus dorsi, but the latter is placed with the extrinsic musculature of the arm for convenience. In *Dipodomys* it was very broad and as an accompaniment of the pronouncedly falcate shape of the Glenovertbral angle of the scapula it overlapped the infraspinatus to a considerable extent. Origin was thus from most of this falcate angle and insertion was along the proximal part of the medial crest of the humerus. In *Scirtopoda* the muscle was hardly one-third as wide as in *Dipodomys*, the origin being correspondingly reduced with the smaller insertion situated more proximally. These features were even more pronounced in *Allactaga*.

Parsons (1894) has said that in *Scirtopoda* insertion of the *teres major* was into the tendon of the latissimus dorsi, but I found the opposite to be the case. He also said that in the *Dipodidae* insertion is posterior to that of the latissimus as in man, but this was certainly not the situation in my specimens. Innervation of the subscapularis and *teres major* is by the subscapular branches of the brachial plexus.

M. deltoideus. In *Dipodomys* the spinal, acromial and clavicular parts of the deltoid comprised a continuous muscle, to all intents homogeneous, but with care they could be separated. The spinal part arose from two-thirds of the spine, and the clavicular from practically the entire clavicle. Common insertion was largely tendinous and rather restricted upon the deltoid crest of the humerus. Conditions in the jerboas were similar save that in *Allactaga* the spinal origin was less extensive and its insertion more individual, passing deep to the acromial part.

M. teres minor. In *Dipodomys* this was partially fused with the infraspinatus. It arose from the distal two-thirds of the Glenovertbral border of the scapula and inserted upon the greater tuberosity caudal to the infraspinatus. This was the case in *Allactaga* and *Zapus* also, but in *Scirtopoda* the muscle was easily separable from the infraspinatus. Origin, however, was only from the distal third of the Glenovertbral border, and insertion in both jerboas was mostly deep to the infraspinatus. Innervation of both deltoid and *teres minor* is by the axillary nerve.

Muscles of the brachium.

Dorsal group.

The triceps complex occurred in four divisions as follows:

M. dorso-epitrochlearis, in *Dipodomys*, was distinct throughout its length, arising chiefly from the *teres major* tendon but to some

extent from that of the of the latissimus as well. It extended broadly over the inner arm to an insertion by fasciculi upon the olecranon. *Scirtopoda* showed to excellent advantage how this muscle may appear by fission from, or disappear by fusion with, as the case may be, the medial surface of the triceps longus. Its superficial aponeurosis was double, one sheet coming from the scapula and the other from the teres major and latissimus tendons. Both shortly fused and passed deep within the substance of the muscle. In other words muscle fibers gradually developed upon the medial surface. This was a condition fairly intermediate between *Dipodomys* and *Allactaga*, in the latter of which there was no connection at all with the teres major or latissimus.

M. triceps longus. In *Dipodomys* this was relatively large. Origin was partly by tendon from the axillary border of the humeral head and partly fleshy, not from the bone but directly from an aponeurosis that passed from the acromion to the deep surface of the teres major and then around the axillary border of the scapula, this part of the origin being more clearly visible from the lateral than the medial side. Insertion was upon the posterior part of the olecranon. In the jerboas the entire origin was broadly tendinous, from the distal quarter of the scapular border.

M. triceps lateralis. In *Dipodomys* origin was by tendon from the lateral part of the humeral head just deep to the insertion of the teres minor, and insertion was upon the ulnar border of the olecranon. In *Scirtopoda* origin was from a trifle farther to the rear on the humeral head, and this was more pronounced in *Allactaga*.

M. triceps medialis. Origin was from the medial crest of the humerus distal to the teres major insertion and along the caudal border of the shaft, while insertion was upon the lateral olecranon.

No true triceps anconeus, either medial or lateral, was present as a separate division.

Innervation of the triceps group is by the radial nerve.

Ventral group.

M. biceps brachii. In *Dipodomys* the long head arose as usual from the bicipital process upon the Glenovertbral border of the scapula, and the short head from the coracoid tip. The tendons remained separate throughout their length, the two partially twisting so that the one belonging to the long head inserted upon the medial ulna with the brachialis, and the other upon the usual area of bicipital attachment of the radius. In the jerboas there was only one head,

as Parsons has stated. This was the long head, even smaller than the corresponding division in *Dipodomys*. Insertion was upon the ulna with the brachialis. In *Zapus* there was also a single head.

M. coracobrachialis. In *Dipodomys*, as well as *Zapus*, a pars profunda, or breve, of the coracobrachialis occurred, arising from the coracoid process and inserting upon the neck of the humerus above the latissimus tendon; but this could not be found in the jerboas,

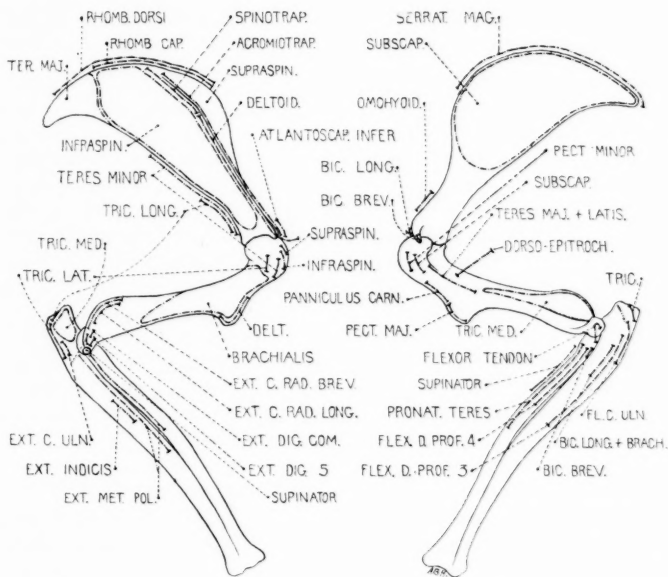


FIGURE 10. The long bones of the anterior limb of *Dipodomys* showing areas, semidiagrammatically, of muscle attachment: lateral (left) and medial views.

although Parsons (1894) stated that he encountered it in *Sciartopoda*. The pars media was represented in all, arising from the coracoid as usual. In *Dipodomys* it was very slender and inserted upon the humerus well below the latissimus tendon. In *Sciartopoda* it was very well marked and inserted from a point somewhat below the latissimus quite to the epicondyle, and similarly in *Allactaga*, save that insertion

began immediately adjoining the latissimus. A relatively large brevis was present in *Zapus*.

M. brachialis. In all three animals this muscle was completely divisible into two parts. The more lateral arose from the surgical neck of the humerus lateral to the deltoid crest, and the medial, more upon the medial aspect of this crest and directly adjoining it. Insertion was upon the ridge on the medial ulna just below the sigmoid cavity, in company with the long head of the biceps.

Innervation of the brachial flexors, comprising the ventral group, is by the musculocutaneous nerve.

Muscles of the antibrachium.

Dorsal group.

M. brachioradialis (supinator longus). Parsons has stated that this muscle is present in most sciurormorphs, but it was absent in *Dipodomys*, as it was in the wood rat. In *Sciirtopoda* it was slender and, as Parsons mentioned, insertion was not upon the radius but upon the medial process at the base of the pollex. In *Allactaga*, however, insertion was upon a process upon the medial side of the distal radius. The muscle was present in *Zapus*.

M. extensor carpi radialis longus. In *Dipodomys* this, the most radial muscle upon the lateral forearm, took origin from the lateral epicondyle partly deep to the brevis and inserted upon the medial base of metacarpus 2. In the jerboas it was smaller and origin was not partly deep to that of the brevis, while insertion was upon the middle of the medial side of metacarpus 2.

M. extensor carpi radialis brevis. In all three animals origin was from the lateral epicondyle distal to, and in *Dipodomys* partly superficial to, origin of the longus. Insertion was upon the lateral side of metacarpus 2.

M. extensor digitorum communis. Origin was narrowly from the lateral epicondyle adjacent to the extensor brevis, and tendons extended to digits 2, 3 and 4. In addition there was a partially separate slip which arose ulnarward from the communis aponeurosis and passed with the other tendons to insert upon the medial side of digit 5. In the jerboas insertion was upon the four lateral digits.

M. extensor digiti quinti. This was slender and arose from the lateral epicondyle and ulnarward of the extensor communis. Insertion was upon the lateral side of digit 5, and in *Allactaga* there was also a tendon to digit 4, the latter running deep to the communis tendon.

M. extensor carpi ulnaris. In *Dipodomys* origin was by two slips, one from the posterior border of the lateral epicondyle and the other from the lateral base of the olecranon. These soon fused and insertion was upon the process at the base of metacarpus 5, as was the case in the jerboas as well.

M. supinator. In *Dipodomys*, origin of this muscle, situated radialward of the extensor metacarpi pollicis, was largely by tendon from the capsule of the joint, but there had developed at this point a well defined sesamoid bone, located directly lateral to the radial head. Insertion was upon the medial aspect of one-third of the dorsal border of the radius. In the jerboas there was no sesamoid, but in *Scirtopoda* there was a well defined lateral process upon the radial head, and in *Allactaga* origin was more definitely from the humerus than in the other two.

M. extensor metacarpi pollicis (abductor pollicis longus). Origin was by two heads, both fleshy, from the proximal third of the latero-ventral shaft of the radius and from two-fifths of the laterodorsal ulna below the joint. These soon joined and the common tendon slanted over the radial border superficial to the two extensor carpi radialis tendons to insert, in *Dipodomys* and *Scirtopoda*, upon the falciform bone of the carpus, rather than upon metacarpus 1. In *Allactaga* the chief attachment was also to the falciform but a tendinous band passed to metacarpus 1 as well.

M. extensor indicis. This was quite slender and situated just deep to the extensor digiti quinti. Origin was from the lateral border of the ulna and in *Dipodomys* this was bound down by a stout ligament which extended from the epicondyle for a considerable distance to an attachment upon the lateral ridge of the ulna. The tendon, passing deep to that of the extensor communis, was inserted mainly upon the dorsum of digit 2, but a slender branch also passed superficial to the extensor carpi radialis longus tendon to an insertion upon digit 1. In *Scirtopoda* the tendon was even smaller and the branch to digit 1 was stouter than that to 2. In *Allactaga* the ligamentous band over origin was not present and insertion was upon the lateral side of digit 2 only.

Innervation of all the muscles of the dorsal group of the anti-brachium is by the radial nerve.

M. pronator teres. Origin was uniformly from the medial epicondyle and insertion upon the proximal third of the radial border of the radius.

M. flexor carpi radialis. Origin was from the common epicondylar

tendon with insertion upon metacarpus 2. In *Scirtopoda* the tendon of insertion was exceedingly slender.

M. palmaris longus. Origin was from the medial epicondyle between the flexores carpi radialis and ulnaris, with insertion into the palmar fascia.

M. flexor digitorum sublimis. Origin was from the epicondyle and apparently the joint capsule, and in *Dipodomys* insertion was upon digits 1 to 4. In the jerboas only digits 2 to 4 were involved.

M. pronator quadratus. In *Dipodomys* there were only a few interosseous fibers representing this muscle, and in the jerboas definition was but slightly better.

Innervation of the pronators, palmaris longus, flexores carpi radialis and digitorum sublimis is by the median nerve.

M. flexor digitorum profundus. In *Dipodomys* and *Scirtopoda* origin was by four heads (1) from the medial epicondyle by means of the aponeurosis common to it and the flexor carpi radialis, (2) from the sigmoid border, (3) a robust head from the medial ulna, and (4) a weak one from the adjoining part of the radius. They joined to form a very heavy tendon, branches of which extended to all five digits. In *Allactaga*, however, no fourth head was detected. Innervation is by both median and ulnar nerves.

M. flexor carpi ulnaris. Origin was from the ventral part of the olecranon and the ulnar border of the ulna, while insertion was upon the pisiform. Innervation is by the ulnar nerve.

M. epitrochleo-anconeus. Whether a triceps anconeus, innervated by the radial nerve, ever occurs upon the medial elbow of rodents as it does in some other mammals (some primates), I have not determined to my own satisfaction. It is only recently that I have concerned myself with this detail, and although authors have almost always, either by direct statement or implication, placed this slip with the triceps group, with radial innervation, in all rodents (including *Dipodomys* and *Allactaga*) in which I have sought the innervation this has been by the ulnar nerve, allocating the muscle with the two muscles of the forearm so served. In all three saltators it was well developed, with a well rounded contour that rendered it impossible to mistake it for a distal continuation of the coracobrachialis, an error easily made in some other mammals. Origin was from the entepicondyle and insertion upon the olecranon.

No dissection of the muscles of the manus proper was attempted in the present connection. It was felt that with such small specimens there would be too large an element of doubt regarding many of the

details and accordingly it was decided to make no attempt to describe them.

B. Pelvic limb.

It is to the posterior extremity to which we turn with greatest interest in any consideration of saltatorial mammals, and this feature will be discussed at some length. In this connection it will be advisable to examine the lumbar plexus (fig. 11). Unfortunately it was found that in the specimens of *Scirtopoda* available the proximal nerves of this plexus were so fragile and so prone to separate into their component fibers that the plan could not be satisfactorily determined.

Dipodomys. N. femoralis was from L. III and IV only. It pierced the psoas major before it appeared, sending twigs to the

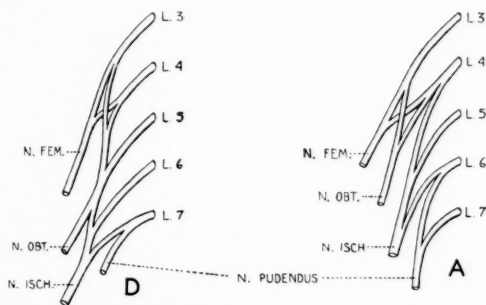


FIGURE 11. The lumbo-sacral plexus of *Dipodomys* (D) and *Allactaga* (A).

psoas, iliacus, and then a number to the pectineus and quadriceps femoris before continuing down the medial thigh as the saphenus nerve. The n. obturatorius was derived from L. III, IV and V. The n. ischiadicus was made up of branches from L. III to VII inclusive, which, for a rodent, appears to be an unusual number of elements. It would, perhaps, be preferable to designate by name the group of nerve twigs from the ischiadicus which serves the hamstring muscles, as these were rather sharply differentiated, but this is not attempted at present. The ischiadicus does not separate to form the tibialis and peroneus communis until well over the hip. The n. pudeneus was weak and came only from L. VII.

Allactaga. In the jerboas the femoral nerve was derived from L. III and IV as well, but instead of piercing the psoas major it emerged between that muscle and the quadratus lumborum. The n. obturatorius was also derived from these roots and had no connection with V. The n. ischiadicus came from L. IV, V and VI only, but the n. pudendus received a minute branch from L. VI, as well as the larger one from VII.

(a) EXTRINSIC SYSTEM.

Dorsal group.

Although the psoas complex is frequently included in the hypaxial system because topographically it is so situated and this course is often convenient, in reality it is a derivative of the extremity musculature and has secondarily invaded this region.

M. psoas minor. The anterior portion of this muscle was so tenuous that it was difficult to decide just where origin began. It may be said, however, that in *Dipodomys* it was from the first three lumbar, while in the jerboas it was more extensive, being from possibly the last thoracic as well as the first four lumbar. A broad, thin tendon developed upon the ental belly and upon this the fibers ended rather abruptly. Insertion was upon the psoas process of the innominate. Innervation is by short branches from the lumbar plexus.

M. psoas major. This muscle was very well developed, although not remarkably so. In *Dipodomys* and *Scirtopoda* origin was from the first five lumbar, while in *Allactaga* the first of these seemed not to be involved. The muscle was not quite so robust in *Scirtopoda* as in the other two animals. Insertion was upon the lesser trochanter of the femur in company with the iliacus. Innervation is by short branches from both the individual trunks of the lumbar plexus and the femoral nerve.

M. iliacus. In *Dipodomys* origin was from practically the whole of the inferior "gluteal" fossa of the ilium as far caudally as just below the rectus process. At insertion fusion with the psoas magnus took place and the whole had attachment to the anterior expanse of the lesser trochanter. In *Scirtopoda* origin was more extensive anteriorly, reaching the crest of the ilium, but the muscle as a whole was less robust. In *Allactaga* it was smaller still, and origin was from the inferior border only of the ilium. Innervation is by the femoral nerve.

(b) INTRINSIC SYSTEM.

Muscles of the hip and thigh.

Dorsal group.

M. vastus lateralis (or *externus*). In *Dipodomys* this muscle was greatly developed as is usual in rodents. It arose from the distal border of the greater trochanter, with insertion upon the patella, and at origin it did not completely cover the vastus medialis. In the jerboas, however, it did cover the latter muscle and the origin was located a trifle more posteriorly. Origin merely adjoined that of the gluteus minimus while in *Dipodomys* the tendon of origin of the latter was superficial to the vastus lateralis at origin.

M. vastus medialis. While this muscle in *Dipodomys* was no more massive than usual it was more extensive at origin. This was not only from the anterior surface of the lesser trochanter and the shaft adjoining, but passed dorsal to the head, onto the greater trochanter and to its caudal border, thus reappearing from beneath the caudal part of the vastus lateralis origin. Fibers of this posterior part inserted upon an aponeurosis that covered most of the vastus femoris, although the main insertion was medially upon the patella. In the jerboas this division was smaller and with origin less extensive.

M. vastus femoris (or *intermedius*). This arose over the anterior shaft both medially and laterally, and insertion may be said to have been upon the capsule of the knee joint, although fibers stopped short of the joint proper, and the muscle must accordingly be considered as a trifle degenerate. At origin the relationship of the more proximal fibers was extremely close with those of the lateralis, so that it was difficult to determine where origin of one left off and the other began. In *Scirtopoda* fibers extended more definitely upon the capsule. In *Allactaga* origin did not extend so far proximal and insertion was more definitely tendinous upon the capsule.

M. rectus femoris. Origin was from the rectus femoris process of the ilium, practically absent in *Allactaga*, and insertion was as usual upon the proximal patella.

Innervation of the vasti and rectus femoris, comprising the quadriceps femoris, is by the femoral nerve.

Usually, in the case of rodents, it is stated that there is a sartorius and a tensor fasciae latae, or when there is no separation, that the two have fused. In discussing the wood rat I pointed out that this mass could not be divided and as there was no innervation by the femoral nerve, the sartorius element must be considered as absent.

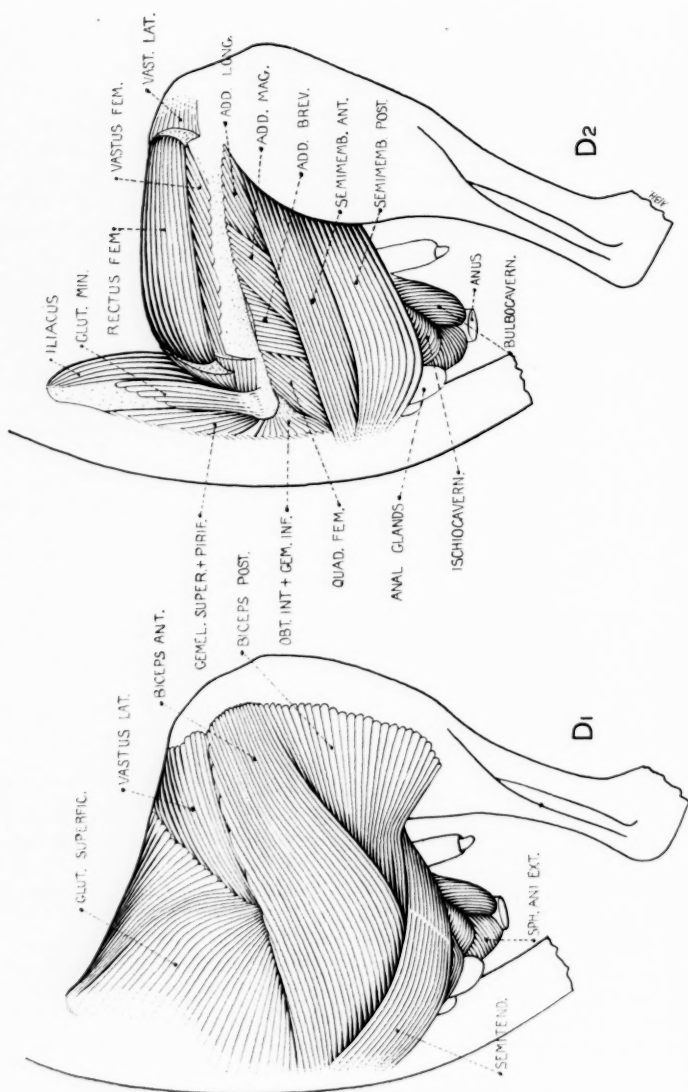


FIGURE 12. Muscles of the right thigh of *Dipodomys*: superficial (D_1) and deeper (D_2) (with gluteus maximus and medius removed) layers.

Innervation was exclusively by the superior gluteal nerve and hence the tensor fasciae latae was the only element present. A similar condition was encountered in the three saltatorial rodents dissected. In three specimens of jerboas and several of *Dipodomys* in which this detail was examined I could discover no service by the femoral nerve and I shall continue calling this sheet as follows:

M. gluteus superficialis. In *Dipodomys* origin was from the dorsal aponeurosis and from the iliac crest, while insertion was toughly upon the proximal part of the lateral femoral crest and the fascia covering the anterior thigh, the muscle fibers not reaching to the knee. Although the appearance was exactly what one would expect to result from fusion of a tensor latae with a sartorius, the evidence, I think, is entirely conclusive that the former element was the only one present, this superficial division of the gluteus mass having been specialized in an interesting manner to assume at least in part the function of a nonexistent sartorius. Attention may also be called to the statement by Parsons (1894) that the sartorius which he found in the rodents he dissected was served by the superior gluteal nerve, showing that this was *not* the element present.

In *Scirtopoda* the superficial gluteus was smaller, and whereas in *Dipodomys* the posterior border was entirely deep to the biceps, in the former it was superficial proximally, only the more distal portion twisting inward to insert, not upon the lateral crest of the femur, which the jerboas lack, but upon the deep aponeurosis between the vasti and the muscles posteriorly situated, and also upon the superficial aponeurosis over the front of the thigh as usual. The anterior part was partially divisible into a slip with a singular resemblance to a sartorius, arising from the inferior iliac border adjoining the crest, thence spreading well over the medial thigh; but absence of femoral innervation and the following of its nerve supply to junction with the ischiadicus proved this resemblance to be only superficial.

In *Allactaga* the lateral area of the muscle was even smaller than in *Scirtopoda* and no part of it was situated superficial to the biceps femoris border. The partially divisible section resembling a sartorius also extended more ventrocaudally upon the ilium, although the belly was less extensive over the medial thigh. The innervation was the same.

The partial division of this sheet in the jerboas is very interesting and illustrative, perhaps, of a rather successful attempt to differentiate a portion of the gluteal mass to take over the needed function fulfilled by a sartorius were one present.

At origin the main gluteal complex was largely inseparable, although the divisions were entirely distinct toward insertion.

M. gluteus medius. This was by far the most massive part of the gluteal complex. In *Dipodomys* origin was slightly from the fascia investing the iliocostalis, but mostly from the anterior part of the superior gluteal fossa of the ilium, and for a short distance ventrally along the crest. Insertion was robustly upon the greater trochanter superior to the vastus lateralis. In the jerboas origin was somewhat less extensive.

M. gluteus minimus. In *Dipodomys* origin was from practically the entire superior gluteal fossa of the ilium and caudally almost to the acetabulum, while insertion was upon the cranial border of the greater trochanter. In *Scirtopoda* origin was somewhat less extensive ventrally, allowing space for the scansorius. In *Allactaga* this division was fused with the gemellus superior and piriformis.

M. scansorius (or *gluteus quartus*). This was present in *Scirtopoda* only, with origin from the ventral part of the inferior gluteal fossa of the ilium with insertion upon the greater trochanter adjacent to the *gluteus minimus*.

Innervation of the above gluteal components is by the superior gluteal nerve.

M. gluteus maximus. In *Dipodomys* origin was mostly from the dorsal fascia above the ilium. It passed posterior to the femoral head as usual and insertion was upon the posterior border of the greater trochanter and distally to the base of the lateral crest or third trochanter. In the jerboas this muscle was smaller and insertion was more toward the base of the greater trochanter. Innervation of the *gluteus maximus* is by the inferior gluteal nerve.

M. piriformis. In all three animals this muscle had experienced at least partial fusion with the gemellus superior. In *Dipodomys* the two were virtually inseparable and the piriformis could be distinguished only by the fact that its fibers arose from the transverse processes of the third and fourth sacral vertebrae. Insertion was by tendon upon the greater trochanter. This was also the case in *Allactaga*, while in *Scirtopoda* separation of all but the insertional tendon was possible. The piriformis is innervated by short branches of the sacral nerves, not detected in the present instance.

M. biceps femoris anticus. This corresponded to the short femoral head in man, for it was served by the n. peroneus communis. It was very robust and in *Dipodomys* was simple, arising from the dorsal aponeurosis over the ischium and inserting upon the patellar

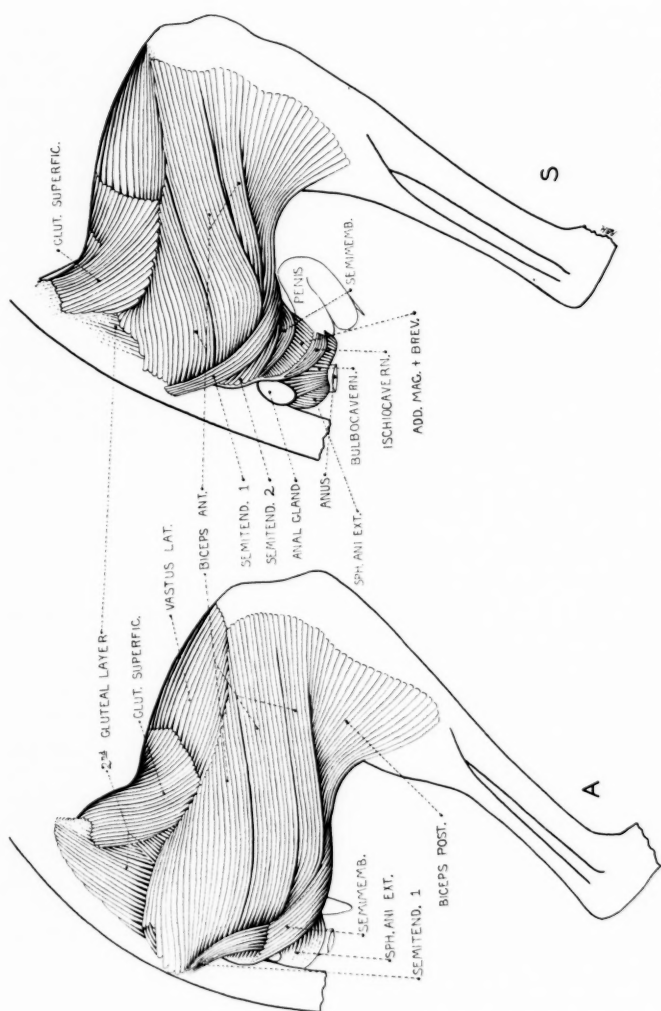


FIGURE 13. Superficial muscles of the region of the right thigh of *Allactaga* (A) and *Scirtopoda* (S).

ligament. In all these rodents the two main heads of the biceps were considered to be distinct throughout their length, although actually their insertional parts were fairly continuous. In the jerboas this part was not only very broad but was divisible (with less ease in *Scirtopoda* than in *Allactaga*) into three portions. The first of these was composed of those fibers which arose from the dorsal fascia and from the aponeurosis between the dorsum and ischium, and inserted upon the deep aponeurosis adjacent to the vasti. The second part comprised those fibers which arose by tendon from the tuber ischii and inserted over the patella; and the third, those fibers farther posterior, arising from the aponeurosis common to this and a part of the biceps posticus, with insertion largely over the patellar ligament. In *Scirtopoda* the first and second of these parts were not surely separable from the posticus. In *Allactaga* the situation was rather peculiar in that only a part of the second division of the biceps anticus came into contact superficially with the semimembranosus, where these bridged over the semitendinosus, and at this point there was definite fascicular fusion of a number of their fibers. Innervation is by a twig diverging from the ischiadicus well above the point where it separates to form the peroneus and tibialis, but its affinity is doubtless with the former.

M. tenuissimus. The phylogeny of this muscle is still undecided but as many anatomists believe that it has been derived from the short biceps it is here placed for the present. It was encountered in *Dipodomys* only, in the long, extremely tenuous form which it invariably assumes. It arose from the deeper dorsal fascia deep to the anterior biceps origin, with fascial insertion upon the medial calf. Innervation is by a long, exceedingly tenuous filament diverging from the ischiadicus well beneath the gluteal mass.

Ventral group.

M. gemellus superior. As previously stated this muscle was almost completely fused with the piriformis. In *Dipodomys* it could be distinguished from the latter only by the fact that it arose from the middle of the superior iliac border as far caudally as the distinctive process there situated, as contrasted to the piriformis origin from the transverse processes. Insertion was tendinous upon the greater trochanter. In *Scirtopoda* origin extended almost to the iliac crest and separation of all but the insertional part was possible. In *Allactaga* fusion with the piriformis, as well as with the gluteus minimus, was more marked.

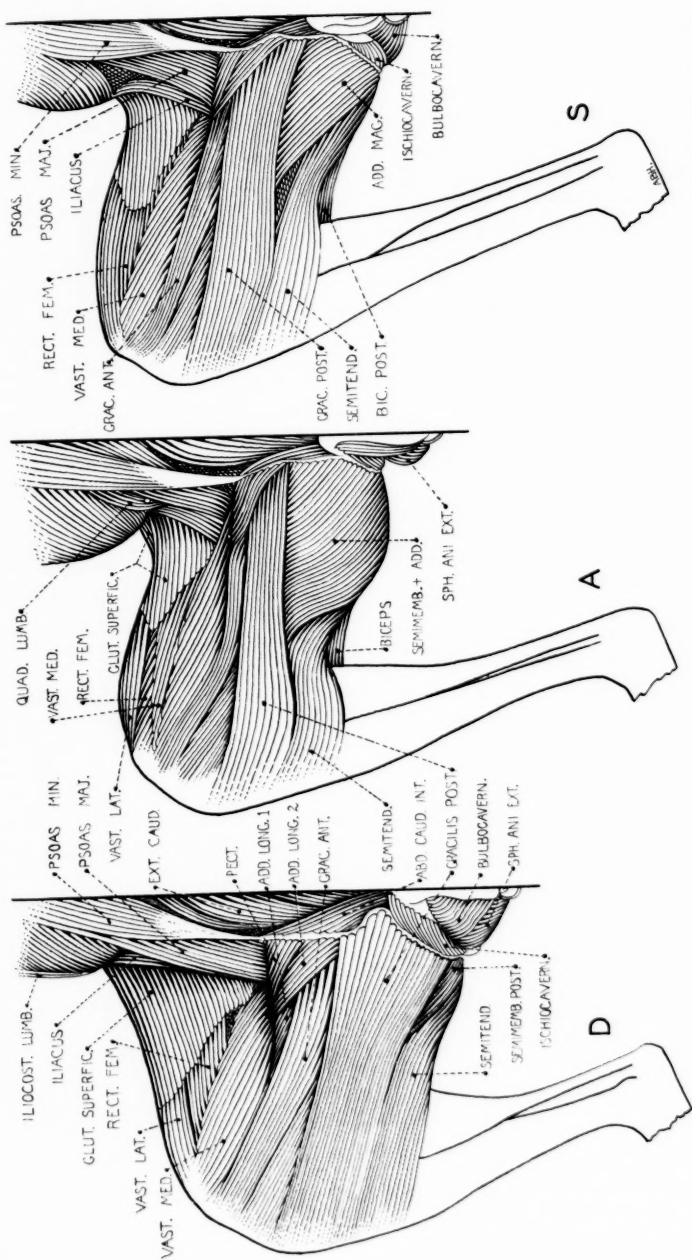


FIGURE 14. Superficial muscles of the region of the right thigh of *Dipodomys* (D), *Allactaga* (A), and *Scirtopoda* (S), from the medioventral aspect.

M. gemellus inferior. The relationship of this muscle with the quadratus femoris and tendon of the obturator internus was very close. In *Dipodomys* the main part of origin was from the ischial border anterior to the notch for the internal obturator tendon, but the muscle had extended slightly to the rear of this point as well, thus covering the obturator tendon and therefore with its fibers originating from the deep sacral fascia. Insertion was upon the obturator tendon. In the jerboas origin was as usual from posterior to the regular position of the obturator tendon (absent in these animals), with insertion more definitely into the obturator fossa of the femur.

M. obturator internus. In *Dipodomys* this muscle was double, just as Parsons (1898) reported in *Pedetes*. The proper, more posterior part was less extensive than usual, covering only the caudal part of the obturator foramen. The accessory part, entirely separate, occupied the well defined fossa situated medial to the acetabulum, and sent a separate tendon over the obturator notch, which was especially well defined in this genus. No muscle fibers could be observed from the lateral side and the two tendons, joining, inserted into the obturator fossa. In the jerboas this muscle was very decadent and the part passing over the pelvic brim had so nearly disappeared that no tendon could be detected.

M. quadratus femoris. In *Dipodomys* this presented the appearance of being in two portions, although in reality these were indivisible, by virtue of the fact that part of the origin was tendinous from the cranial part of the lateral tuber ischii ridge, while insertion was fleshy upon the proximal base of the third trochanter. In the remainder of the muscle these conditions were reversed, for origin was fleshy and extensive, from almost all of the ischium posterior to the obturator foramen, while insertion was tendinous upon the lesser trochanter and its proximal ridge. In the jerboas this condition did not obtain and the muscle was simple in appearance; nor was it so robust as in *Dipodomys*. Origin covered about the same area but insertion was only upon the tip of the lesser trochanter.

The gemelli, internal obturator and quadratus femoris are all served by short twigs of the ischiadicus.

M. semitendinosus. This muscle arose by two heads. In *Dipodomys* origin of the fascial head was from the dorsum, and of the ischial, from the tuber. They shortly fused and there then occurred a completely transverse aponeurotic inscription. From this the main portion of the muscle continued to the medial calf, but there was

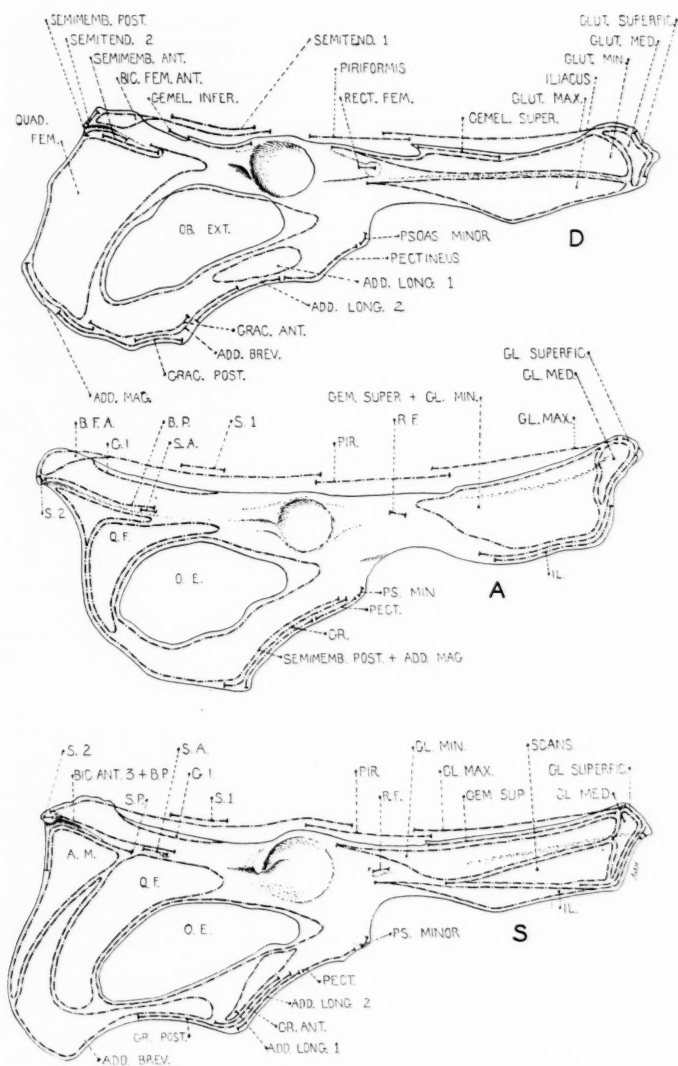


FIGURE 15. Right innominate bone of *Dipodomys* (D), *Allactaga* (A), and *Scirtopoda* (S) showing, semidiagrammatically, the areas of muscle attachment.

a small slip which diverged to fuse with the posterior biceps and pass to the lateral thigh. It is interesting to note that a precisely similar slip was encountered in the sea otter (*Enhydra*). In the jerboas there was no transverse aponeurotic inscription. Save for being narrow conditions were otherwise essentially similar in *Scirtopoda*. In *Allactaga*, however, as the superficial division crossed the ischial border it disappeared from sight between the semimembranosus and the biceps, reappearing once more from between these muscles upon the middle of the thigh, where the superficial head joined the deeper head. The origin of the latter was not only completely hidden by the other division, but even after removal of the latter practically none of the deeper division could be seen, because situated mostly deep between the semimembranosus and the biceps.

M. semimembranosus. In *Dipodomys* this also occurred in two divisions. Pars postica, the larger (about as in *Neotoma*), arose from the ischium along the lateral ridge extending from the tuberosity. Upon the medial aspect of the limb it passed deep to the gracilis and inserted by fascia upon the distal part of the patellar ligament. Pars antica arose slightly below (deep to) and anterior to the postica origin. Although origin was by a single aponeurosis there were really two divisions of this part, the larger and more medial inserting fleshily under cover of the anterior gracilis upon the medial epicondyle of the femur, and the second slip upon the base of the femoral shaft adjacent to, but more toward, its lateral side.

In *Scirtopoda* both divisions were small but distinct. Origin of the more posterior was from the ventral ridge of the tuber ischii and ventrally slightly along the caudal border of the bone. Origin of the anterior division was by a slender tendon from the cranial part of the tuber ridge. It then divided into two small slips, the more lateral inserting upon the posterior part of the extreme distal femoral shaft and the other more medially. In *Allactaga* a peculiar condition was encountered. It was possible easily to differentiate a single anterior division, thin but with very coarse fibers extending from the ischium to the femoral shaft, like the more superficial division of *Scirtopoda*, but here differentiation ceased. The fibers were so coarse and loose that perfect separation was possible at many points, but all were parallel and although it was possible to distinguish the different elements present, the posterior semimembranosus and all of the adductors proper had to all intents become one powerful muscle and must so be treated. Parsons mentioned the partial blending of the

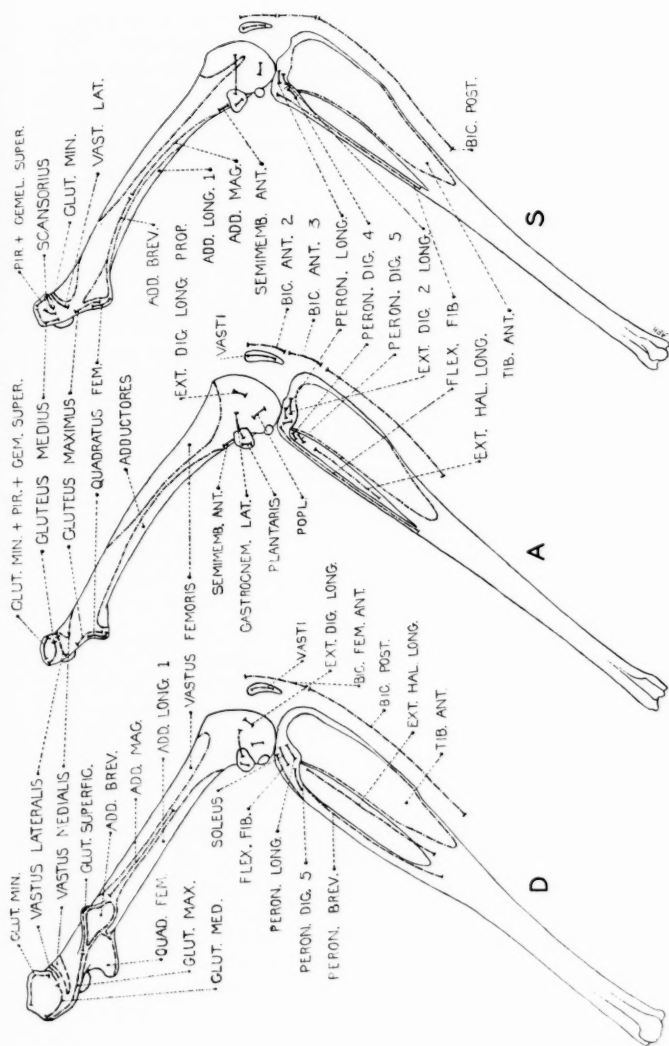


FIGURE 16. Lateral aspect of the bones of the right thigh and shank of *Dipodomys* (D), *Allactaga* (A), and *Scirotopus* (S) showing the areas of muscle attachment.

several elements in *Scirtopoda* but the tendency seems to culminate in *Allactaga*. The details will be presented under the adductors.

M. biceps femoris posticus. In *Dipodomys* this arose narrowly by aponeurosis from the tuber and spread to an insertion over the shank, as illustrated (fig. 12). It should be noted that in this division the origin was narrow and insertion broad, while in the anterior biceps the opposite condition prevailed. In the jerboas this posterior part was very narrow.

Innervation of the semitendinosus, semimembranosus, and biceps posticus is by twigs of the ischiadicus which separate high up on the trunk and pass deep to the origin of the anterior semimembranosus before joining the muscles.

Mm. adductores femoris. The femoral adductors of rodents often prove to be very exasperating for the reason that there appears to be no certain manner in which they can be homologized with the accepted longus, brevis, and magnus divisions of man. *Dipodomys* was no exception to this rule, but if it were not for the short slip adjacent to the pectineus, in position and appearance from the superficial aspect entirely similar to the human adductor longus, matters would be simple, for it is possible to distinguish three other adductor divisions which conform essentially to human conditions. As one of these, deep to the questionable slip, is a perfectly good longus I am of the opinion that the former comprises an accessory muscle, but whether it be a derivative of the pectineus or of the true adductor longus I am not prepared to say. Perhaps this is not of great moment, for the part of the pectineus innervated by the obturatorius is nothing but a part of the adductor complex. At any rate I shall for the present retain for this questionable slip the term adductor longus, but with the qualitative term *accessorius*, while for the deeper and more extensive division which in other respects conforms in better degree to the human longus, I shall adopt the name adductor longus *primus*.

The adductor magnus was the most laterally situated. In *Dipodomys* this arose from the caudoventral part of the ischial border and it inserted upon the femoral shaft distal to the third trochanter for about three-fifths of the distance therefrom to the condyle. In *Scirtopoda* origin was from the entire caudal border of the ischium ventral to the tuber ridge, this being more dorsal than in *Dipodomys*. Insertion was upon the shaft over the distal half of the femur. This is a compound muscle, served by both the ischiadicus and obturatorius.

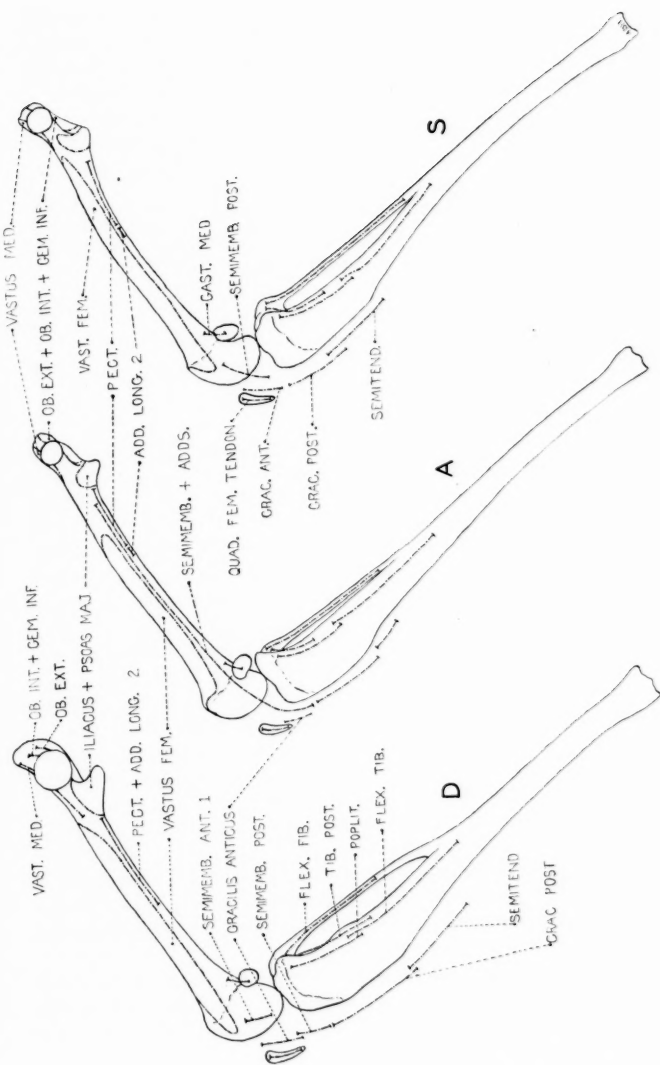


FIGURE 17. Medial aspect of the bones of the right thigh and shank of *Dipodomys* (D), *Allactaga* (A), and *Scirtopoda* (S) showing the areas of muscle attachment.

The adductor brevis was extremely robust in *Dipodomys*, although origin was thinly from the ventral ischial border between the adductores longus accessorius and magnus, with insertion robustly upon the caudal surface of the third trochanter. In *Sciuripoda* it was also massive, with origin from the ventral two-thirds of the caudal ischial border and almost as far cranially as the symphysis, and insertion upon the proximal half of the femur to and including the caudal surface of the lesser trochanter.

The adductor longus primus arose in *Dipodomys* along the pubic border from the adductor brevis to the pectineus and deep to the longus accessorius and a part of the gracilis anticus, while insertion was along almost the entire shaft of the femur. In *Sciuripoda* the gracilis origin had more thoroughly invaded the space between the two divisions of the longus, but origin was from a comparable area, and insertion was distal to the lesser trochanter for half the distance to the condyles.

The adductor longus accessorius resembled only from the superficial aspect the adductor longus of man, for it was very thin, arising along the pubic border caudal to the pectineus. In *Dipodomys* it ended in a slender tendon which joined the distal part of the pectineal tendon. In *Sciuripoda*, however, the tendon did not actually join that of the pectineus but inserted with it at a point about two-fifths of the distance distally upon the femoral shaft. This slip is served by a twig of the obturator nerve, labelling it indubitably as one of the adductors.

In *Allactaga*, as mentioned previously, the adductor complex and the posterior semimembranosus had experienced such a complete degree of fusion that it was impracticable to separate the component parts with any measure of satisfaction. The whole constituted a very robust muscle arising (the semimembranous part) from the ischium ventral to its tuber ridge and around the ventral border to the pubis at the anterior part of the symphysis. Here, however, origin of the adductor longus accessorius was distinct. Insertion of the semimembranous part was upon the medial epicondyle of the humerus, its fascia continuing onto the tibial head, while attachment of the adductor part continued therefrom proximally along the caudal border of the femoral shaft to and including the lesser trochanter.

M. gracilis. This was double in all three rodents. In *Dipodomys* the posterior division, which was extensive, originated along the caudoventral border of the ischium as far as the anterior part of the

symphysis, with insertion along the shank over an area proximal to the semitendinosus, practically as far as the patellar ligament. Origin of the more anterior part was hidden by the adductor longus accessorius and the posterior part by the posterior gracilis. Insertion was upon the patellar ligament cranial to the semimembranosus posticus. Although in *Scirtopoda* the fascia of origin of the posterior gracilis extended as far caudally as in *Dipodomys*, muscle fibers did not begin until farther cranially. Also insertion differed in that it extended deep to a considerable portion of the visible adductor longus. Origin of the anterior division was entirely deep to the posterior, while insertion was the same as in *Dipodomys*. In *Allactaga* even a greater area of the posterior aponeurosis of origin was devoid of muscle fibers.

M. obturator externus. This arose from all of the margin of the obturator foramen except the extreme cranial portion. Insertion was into the trochanteric fossa of the femur.

Innervation of the adductor group, including gracilis and obturator externus, is by the obturator nerve. I hesitate to deny that the adductor magnus was served also by the ischiadicus, but I failed to detect this in the specimens examined.

Dorsoventral complex.

M. pectineus. This is believed to be a compound muscle, its components derived from a dorsal and a ventral element, because innervation is by the femoral, and in most cases by the obturator nerve as well, although it is stated that the latter service is often lacking in man. Twigs from both were demonstrated to occur in *Dipodomys*. Origin was as usual for a short distance along the ventral pelvic border immediately caudal to the psoas process, and insertion was along the proximal part of the femoral shaft.

Muscles of the crus.

Dorsal group.

M. peroneus longus. Origin in *Dipodomys* was from the fibular head in intimate connection with the collateral ligament. Its tendon passed behind the outer malleolus and thence under the peroneal retinacula and between metatarsus 5 and the cuboid, to insert upon the plantar process of metatarsus 1. In *Scirtopoda* this was the smaller of the two peronei, with origin partly fleshy and partly tendinous, the latter giving the appearance of being a direct con-

tinuation of a portion of the collateral ligament. The tendon continued to the sole through a groove formed by a well defined process of metatarsus 4 and the cuboid, and this was covered by the lateral tarsal sesamoid. Insertion then was upon the lateral side of the high plantar process of metatarsus 1. Except for the fact that in *Allactaga* no part of the origin appeared to be a continuation of the collateral ligament the situation was similar to that in *Scirtopoda*.

M. peroneus brevis. In *Dipodomys* origin was from the medial border of the fibula for its entire length and continuing onto the tibia at the junction of the two bones, while insertion was upon the base of metatarsus 5. The muscle was absent in the *Dipodidae*.

M. peroneus digiti quarti. In *Dipodomys* this arose from the caudolateral belly of the peroneus digiti quinti and its tendon passed beneath those of the latter muscle and extensor digitorum longus to the lateral side of digit 4, inserting upon the second phalanx. In *Scirtopoda* origin was from the cranial border of the fibular head and slightly from the interosseous membrane, and the tendon experienced a definite thickening just before reaching the digit. In *Allactaga* origin was hardly separable from the peroneus digiti quinti.

M. peroneus digiti quinti. In *Dipodomys* this may be considered to arise from the proximal fibular shaft, although relationship here was very intimate with the other peronei. Insertion was upon the lateral side of digit 5, at the terminal phalanx. In *Allactaga* conditions were much the same, but the muscle does not occur in *Scirtopoda*.

Innervation of the peroneal group is by the superficial peroneal nerve.

M. tibialis anterior. In *Dipodomys* this muscle was very robust. It arose from the entire tibial fossa, very deep, upon the lateral aspect of the bone. Its heavy tendon passed beneath the exceedingly stout transverse ligament of the ankle (Lig. transversus cruris) and then to the medial ankle, beneath another but smaller ligament in company with the tendon of the extensor hallucis, and to insertion upon the middle of metatarsus 1.

In *Scirtopoda* conditions were similar except that at the transverse ligament there was a deeper retaining groove and insertion was upon the distal end of metatarsus 1. The muscle was larger in *Allactaga*. At insertion the tendon divided into two, but one branch did not go to the internal tarsale as Parsons (1894) stated is the case in mammals with a hallux.

M. extensor digitorum longus. In *Dipodomys* origin was by tendon from the lateral epicondyle of the femur near the patellar ligament.

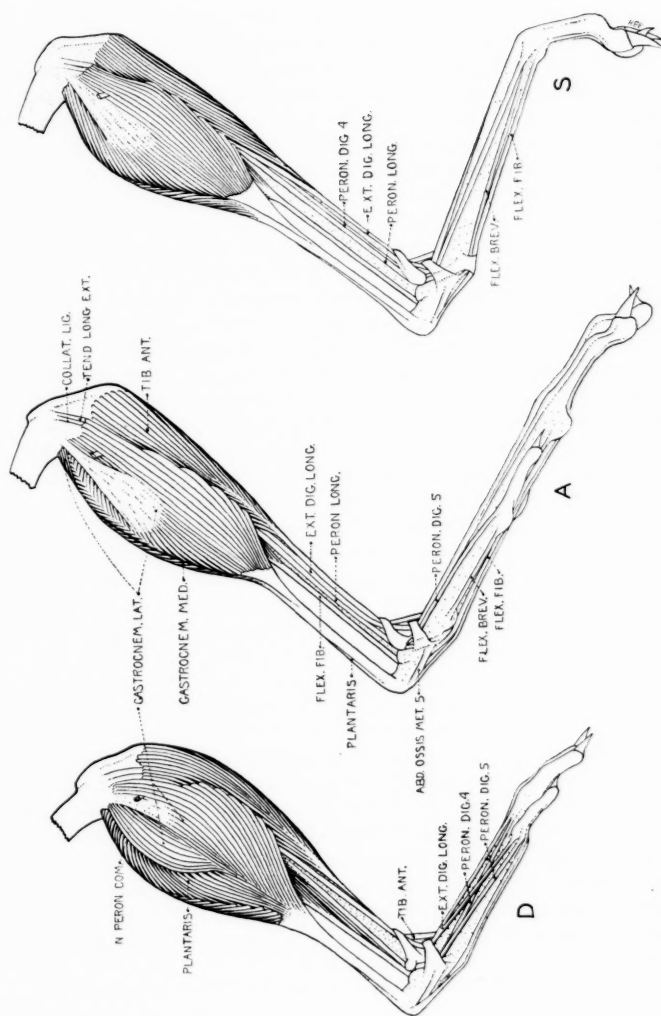


FIGURE 18. Lateral view of the superficial musculature of the right shank and foot of *Dipodomys* (D), *Allactaga* (A), and *Scirtopoda* (S).

The tendon extending from the muscle split almost immediately into four branches, passed beneath the transverse ligament in company with the tibialis anterior and extensor hallucis, and extended to the four toes, these branches being superficial to the other tendons and bound down by the fasciculi transversi which connect the extensor hallucis with the peroneus digiti quarti. The main tendons joined the toes upon the lateral side of digit 2, center of 3, and medial side of digits 4 and 5; but the tendon passing to digit 2 gave off a smaller, lateral branch, and that of digit 4 a medial branch, both of which were attached to the sides of digit 3.

Not only were the tendons of the extensor longus which passed to the three toes of *Scirtopoda* perfectly separable throughout their length, but this was also the case with the muscle. These divisions may be described as follows: The extensor digiti secundi longus arose from the cranial aspect of the fibula and was the most cranially situated of the three divisions. Its tendon passed with those of the other two and with that of the tibialis anterior beneath the transverse ligament. Near the toes the three tendons were confined by a thin, tendinous band or vincula, and the one to digit 2 then diverged to the medial side of the toe, but split into two parts at the metatarsal-phalangeal joint, the more medial of these inserting upon the second phalanx and the other upon the third. The extensor digiti tertii longus was situated next caudalward. It arose from the aponeurosis of the third extensor division near the fibular head. The fleshy part was weak and short, and of the crural part fully two-thirds consisted of tendon. Upon the foot the latter passed deep to that of the third division, and beneath the binding ligament near the toes was ensheathed by it. It emerged once more at the base of the third toe and inserted upon the terminal phalanx. The extensor digitorum longus proprius evidently constituted the main part of the long extensor trinity, for it arose by a stout tendon from the lateral epicondyle of the femur. Its tendon passed beneath a strong ligament that stretched from the fibular head to the tibia. At the base of the toes the tendon split, one branch going to the lateral side of digit 2, and the other to the medial side of digit 4, insertion being upon the terminal phalanx. All these tendons were located lateral to the middle of the tarsus, to a strikingly noticeable degree.

In *Allactaga* there were four divisions of the extensor longus muscle. The transverse ligament of the ankle was much more gristly than in *Scirtopoda* and the bony pulley was better developed. The ligamen-

tum cruciatum was also considerably tougher. As the tendons passed along the dorsum of the foot they were situated even more pronouncedly to the lateral side. The extensor digiti secundi longus arose from the tibial head adjacent to the fibula and its slender tendon passed to the medial side of digit 2 and thence, without splitting, to the second phalanx. The extensor digiti tertii longus was as in *Scirtopoda*. The extensor digitorum longus proprius was from the femoral epicondyle, as in *Scirtopoda*, but at the base of the toes the tendon was broader and thinner. It there split into four branches, the two middle ones, to either side of digit 3, appeared to insert upon the second phalanx, while the two others, along the lateral side of digit 2 and the middle of digit 4 respectively, inserted upon the terminal phalanx. The extensor digiti quinti longus diverged from the tendon of origin of the proprius. It was an exceedingly tenuous slip with thread-like tendon to the second phalanx of digit 5.

M. extensor hallucis longus. I prefer to retain this name for the present muscle even though the kangaroo rat dissected has no hallux. It was an exceedingly slender slip arising in *Dipodomys* from the crural interosseous membrane. Its tendon passed beneath the transverse ligament and then diverged with, but cranial to, the tibialis anterior tendon to the medial side of the foot. It then passed beneath a binding ligament near the first metatarsal and extended to the medial side of digit 2, with attachment to the second phalanx. Over the middle of the pes the tendon was joined to that of the peroneus quarti by fasciculi transversi. In *Scirtopoda* the muscle was absent. In *Allactaga* it was even smaller than in *Dipodomys*. As the tendon passed over the ankle it was situated *posterior* to that of the tibialis anterior, and insertion was upon the second phalanx of the hallux.

Innervation of the tibialis anterior, extensores digitorum longus and hallucis longus, is by the deep peroneal nerve.

Ventral group.

Mm. gastrocnemii. In *Dipodomys* these were large and robust. The lateralis arose from the lateral epicondyle of the femur and the lateral sesamoid. At the center of its superficial belly the origin was tendinous, and this diverged to form a small aponeurotic sheet. The fibers posterior to this aponeurosis were not separable near origin but they were toward insertion, and attached to one side of a deeper aponeurosis while the remaining fibers inserted upon the other side of it. Some of these more posterior fibers also had,

near their origin, close connection with the medialis, thus suggesting the condition, presumably more primitive, existing in the jerboas. The medialis was much the same as the lateralis save that origin extended for a short distance proximally along the shaft of the femur, and the superficial aponeurosis was more extensive. The deep aponeurosis of the two divisions was just as intricate as in most rodents and fairly continuous with the deep aponeurosis of the plantaris. Just proximal to the true tendon the two aponeurotic sheets fused inseparably and the calcaneal tendon passed to the lateral side of the heel. Just above the latter there occurred a thickening of the tendon for a distance of 3.5 mm. this being attributable to a tendency toward the formation of cartilage, which had not progressed as far as calcification.

In *Scirtopoda* this mass was relatively less robust, with the lateral aponeurosis more extensive and coming more sharply from the lateral sesamoid. The medialis was a trifle smaller than the lateralis and the aponeuroses of the two did not fuse until some 7 mm. distal to the beginning of the true tendon. In the jerboas a part of the lateralis, with fleshy origin proximal to the aponeurotic part, curved to the back of the calf and separated, finally to insert upon the deep aponeurosis of the medialis. This slip was pierced by the twigs of the tibial nerve which served the remainder of the lateralis. Such intimacy of relationship between the fibers of the two divisions is a reflection of conditions that are primitive in certain respects. This slip might in reality be called a gastrocnemius tertius (Frey, 1919). In *Scirtopoda* the stiffening of the distal calcaneal tendon was more pronounced than in *Dipodomys*, with a length of 7 mm., and cleaned skeletons show that calcification has occurred within this more rigid portion for a distance of some 3 mm. In *Allactaga* the lateralis was very slightly less bulky but with the superficial aponeurosis more extensive. Other conditions were entirely comparable with those in *Scirtopoda* except that calcification in the distal calcaneal tendon was farther advanced, with a length of 7 mm. Parsons (1898) has stated that in certain kangaroos and in *Pedetes* the lateral gastrocnemius arises from the outer side of the patella, and reached the conclusion that this is a saltatorial modification.

M. soleus. In *Dipodomys* the tendon of origin, from the fibular head, was relatively no longer than in the average rodent. Distally the tendon of insertion fused with the common gastrocnemial tendon at about the middle of the latter. In the jerboas the tendon of origin was considerably longer, while there was no tendon of insertion,

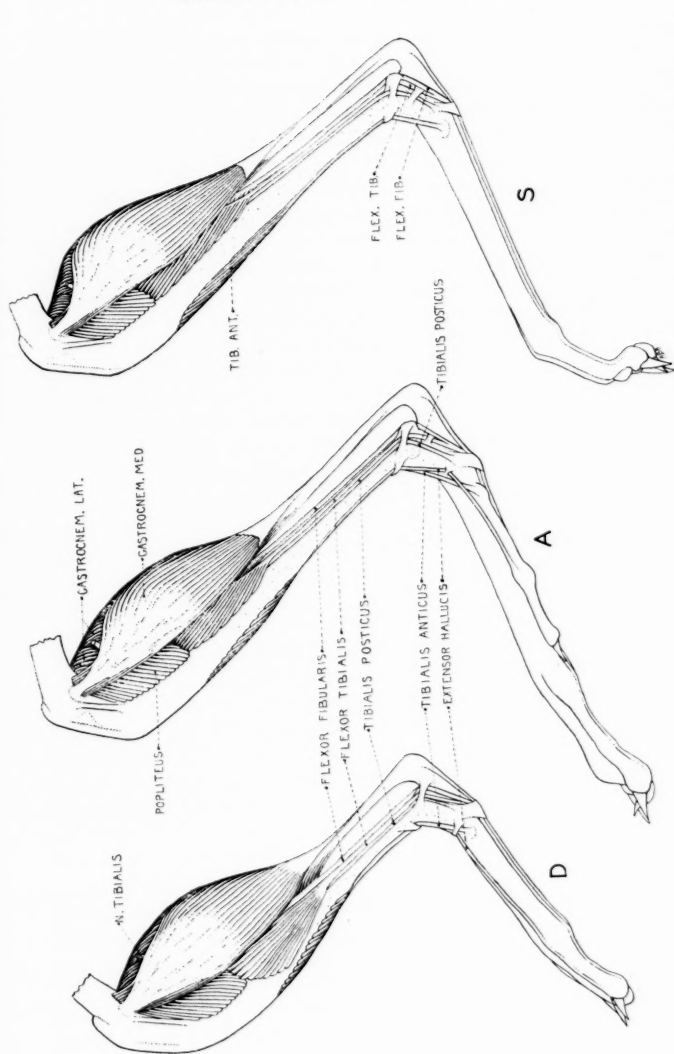


FIGURE 19. Medial view of the superficial musculature of the right shank and foot of *Dipodomys* (D), *Allactaga* (A), and *Scirtopoda* (S).

attachment of the muscle fibers being directly upon the deep aponeurosis of the lateral gastrocnemius.

M. plantaris. In *Dipodomys* tendon fibers at origin, from the lateral sesamoid, were hardly separable from those of the gastrocnemius lateralis, and its aponeurosis also was fairly continuous with that of the gastrocnemius. It was less than half the bulk of either division of the latter, however, and was thus entirely hidden. Its tendon passed medially and then around the gastrocnemial tendon, over the heel and to the sole beneath a binding ligament ventral to the tarsus. It then split into four true tendons, without intervening fasciculi transversi. Those to the three medial digits were robust, the one to the second appearing from the deep aspect of the common tendon, and each of the three was perforated at the base of the first phalanx to allow the emergence of the flexor fibularis tendon; and attachment was to the base of the second phalanx. The tendon to the fifth toe, however, was much more slender than the others and was not perforated, but merely passed to the lateral side of the digit.

In the jerboas the crural part of this muscle was much the same as in *Dipodomys*. Upon the sole the tendon did not divide into its three branches until it reached the base of the three terminal toes. Near this point it first broadened and the middle branch was partially deep to the other two. Each was perforated as in *Dipodomys*. The branches were much broader in *Allactaga* than *Scirtopoda*, however.

Dobson (1883) has stated that there is no flexor digitorum brevis in *Scirtopoda* (his *Dipus*), and he appears to have indicated the same condition for *Allactaga* and *Dipodomys*. True, in these saltatorial rodents this muscle does not appear as a separate unit. The perforation of the terminal plantaris tendons, however, indicates very clearly that this element is definitely present but that its muscle fibers have diappeared and the remainder become entirely fused with the plantaris.

M. popliteus. Origin was by tendon, in which there was a well formed sesamoid bone, from the lateral epicondyle of the femur beneath the extensor digitorum longus tendon. It diverged, binding down the origins of the long flexors, and inserted upon the border of the popliteal fossa, rather poorly defined, over the area indicated in the illustration (fig. 17). In the jerboas the muscle was a trifle smaller than in *Dipodomys*, with the sesamoid also smaller.

M. tibialis posterior. This was extraordinarily weak and the relationship of its fibers with those of the popliteus was close. Origin

was from the fibular head, interosseous membrane, and posteromedial tibial border, partly deep to the popliteus. Its exceedingly slender tendon passed to the medial malleolus just cranial to the flexor tibialis tendon, with the latter through its groove and to the medial tarsal sesamoid. In the jerboas it was even more slender than in *Dipodomys*—nothing but a thread of a muscle.

M. flexor tibialis (flexor digitorum longus). In *Dipodomys* this was very slender, with tenuous origin from the medial tibial border mostly distal to the popliteus insertion. The tendon passed behind a groove on the medial malleolus and fused with the flexor fibularis tendon. In the jerboas conditions were similar save that fusion with the fibular flexor was not complete for some distance after the two met. I thought that in *Allactaga* the tendon fibers might possibly extend to the hallux but upon tearing the two apart I found that this was not the case.

M. flexor fibularis (flexor hallucis longus). This was the chief muscle concerned with the (largely) involuntary flexure of the toes accompanying flexure of the shank. In *Dipodomys* conditions were similar to those occurring in many rodents. The muscle was relatively very powerful and several times larger than the two other long flexors combined. Origin was from the fibular head medial to the soleus and distally along the shaft, from the interosseous membrane, and from the medial aspect of the posterior shaft of the tibia. The very broad tendon which was developed well proximally passed over the medial malleolus and so to the sole, deep to the plantaris. At about the middle of the sole it split into four very heavy tendons which, passing through the perforations of the plantaris tendons, were inserted upon the terminal phalanges. In the jerboas the situation was largely the same, but the muscle was less robust and with a smaller tendon. Like the plantaris the tendon to the three middle toes was single as far distally as the digital articulations. In *Allactaga*, however, a very slender branch diverged well proximally upon either side to join digits 1 and 5.

Innervation of the muscles of the ventral group of the crus is exclusively by the tibial nerve.

Muscles of the pes.

It is always possible, in the case of small rodents, that an investigator has overlooked muscle remnants represented by vestigial fibers, but the following were indubitably present in the three genera dissected.

M. flexor digitorum brevis. This was represented by tendons in fusion with the plantaris, as described under the latter muscle.

M. abductor ossis metatarsi quinti. In *Dipodomys* this was chiefly tendinous and joined the calcaneum to the lateral process of metatarsal 5. In *Sciurtopoda* it was more truly tendinous, to the vestige of the fifth metatarsal, while in *Allactaga* degeneration of the muscle had progressed even further and it occurred as little more than a ligamentous band.

Mm. lumbricales. In *Dipodomys* these were three in number, very tenuous, in the three intervals between the flexor fibularis tendons. *Allactaga* had two of them, well defined, but they had disappeared in *Sciurtopoda*.

Mm. contrahentes digitorum. In *Dipodomys* there were two of these present. They arose by aponeurosis chiefly from the plantar process of the navicular. One was thread-like and extended to the inner side of digit 2, while the other was considerably larger and passed near insertion deep to the short flexor of digit 4, with attachment to both sides of the toe. The fact that insertion was deep (dorsal) to the short flexor introduced an element of doubt about the homology of this slip, but otherwise the two constitute perfectly good adductores digitorum secundi and quarti. Contrahentes were entirely lacking in the jerboas.

Mm. flexores breves (not flexor digitorum brevis). In *Dipodomys* there was a short flexor to each toe, with insertion upon both sides of the digit. The secundi arose mainly by a short tendinous slip from the navicular with an accessory fleshy origin apparently from the inner termination of the first metatarsal. In this connection it should be mentioned that it is extremely difficult, and often impossible, to be entirely positive of the precise tarsal bone to which these short muscles, in a rodent of such small size, are attached. The short flexor to digit 3 arose apparently from the cuboid, while those to digits 4 and 5 originated from the lateral sesamoid, situated plantarward from the base of metatarsus 5. In *Sciurtopoda* the short flexors were represented by three stout tendons devoid of muscle fibers and arising from the lateral sesamoid of the tarsus. Origin of the one to digit 4 was the most ventral, and to the second, most dorsal. The one to digit 3 was of medium size and did not split until it reached the metatarsal-phalangeal sesamoid. The other two, however, both split at about one-third of the distance from the heel to the toe, sending a very robust branch to the inner, and a much weaker one to the outer, side of the respective digits. In *Allactaga* also muscle

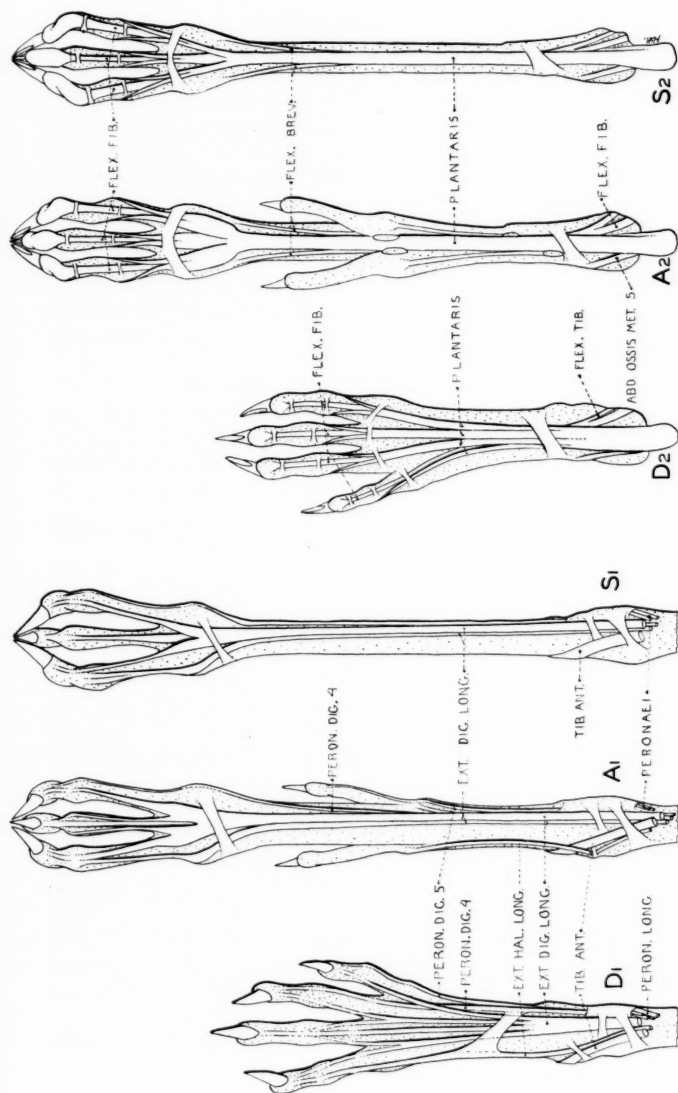


FIGURE 20. Details of the tendons of the pes of *Dipodomys* (D), *Allactaga*, (A), and *Scirtopoda* (S): Dorsal aspect to the left (1), and ventral on right (2).

fibers had disappeared. The first and fifth were very slender and the other three, especially those to digits 2 and 4, very robust. Those to the first three digits arose from the much enlarged sesamoid at the base of metatarsus 1, and the other two from the slightly smaller sesamoid at the base of metatarsus 5, somewhat more posteriorly located.

Innervation of the short plantar muscles is by branches of the plantar nerves, from the n. tibialis.

OSTEOLOGY.

In the osteological portion of the present contribution the skull will be considered on a slightly different basis from the remainder of the skeleton, the former being accorded more lengthy treatment for the reason that few rodents in existence have a cranium more peculiarly and interestingly modified than *Dipodomys*.

The illustrations doubtless give a better idea of skull form than can a description, but nevertheless the general and chief characters of the *Dipodomys* skull in comparison with that of a rodent of typical murine form should be briefly presented. For the latter a small skull of *Neotoma*, with condylobasilar length about equal to the same measurement in *Dipodomys spectabilis*, will be selected.

SKULL.

The preorbital part of the skull of *Dipodomys* is longer than in *Neotoma* and the postorbital part correspondingly reduced. The shape is strongly triangular, with great width through both the mastoid and prezygomatic sections. The interorbital width has also increased, being more than twice as great as in the wood rat. The dominant character of the entire skull is the great size of the mastoid bullae.

In lateral aspect it is seen that the nasals of *Dipodomys* project especially far beyond the incisors, that the infraorbital foramen is located far forward upon the side of the rostrum instead of at the medial base of the maxillary root of the zygoma, and that the latter feature is much broader. Instead of the zygomatic width being the greatest transverse measurement of the skull, as in most rodents, this is surpassed both anterior and posterior to the orbit. Because of the crowding of the mastoids the architecture of the squamosal is greatly altered, and similarly the interparietal and occipital have been much restricted.

The incisive foramina are minute and the choanae much reduced

in size, while the parapterygoid fossae are somewhat more capacious and each is perforated by a foramen of relatively large size. The cornua of the auditory part of the bullae meet in the posterior pterygoid region, and the inflated mastoid part have not only crowded extensively onto the dorsal surface of the skull, but overhang to the rear, projecting considerably posterior to the plane of the occipital.

In final analysis the modifications which the bones of the mammalian skeleton, other than the skull, have undergone are mostly, and indeed almost entirely, attributable to muscle stress. True, there have been mechanical stimuli of a variety of sorts. If there were rodents comparable in size to an elephant they would of necessity have a skeleton much different from that of a mouse, partly in order to support a great weight; and peculiar skeletal modifications often are correlated with special habits. But on the whole such differences must accompany, even though they may not be directly caused by, muscular specialization. This broad generality cannot be applied to the skull, however. In fact it is probable that other stimuli operating for cranial form are considerably stronger than muscle stress. There are the correlated factors of feeding habits and character of dental armature, sensory (including olfactory, ocular and auditory) requirements, and cerebral needs. All these must be nicely adjusted for proper interaction, as a properly formed scaffold for the respective organs, and so that the controlling musculature shall be well suited, in form and position, to operate with the requisite efficiency. When the vital cranial equipment is well balanced for a particular norm one encounters a skull suited to the needs of a generalized type varying with the requirements of particular groups of mammals—an "average" rodent skull, or that of a carnivore, or insectivore, or ungulate. If one of the factors of the vital cranial equipment depart widely from its norm for the particular type concerned, it will affect the entire skull to a greater or lesser degree, according to the quality and quantity of the alteration. Some of these changes are quite simple, affecting in appreciable extent only a single detail, while the surrounding bony topography is insignificantly altered. Others may be very complex, causing profound alteration in many features of the skull. In the latter category is the development of the audital bullae of *Dipodomys*, and the parallel feature in certain of the jerboas. This has had a very pronounced effect upon the skull and, fortunately, the successive steps by which the present conditions were attained may be followed with a considerable degree of assurance through other, more generalized forms of the Heteromyidae.

The above steps, leading to extreme hypertrophy of the bullae, are nicely illustrated by the following skulls, figured on page 479: *Liomys irroratus*, *Perognathus (Chaetodipus) baileyi*, *Perognathus (Perognathus) amplus*, *Dipodomys spectabilis*, and *Microdipodops pallidus*. With *Dipodomys* are also compared certain features of the species of jerboas which are available, and of the wood rat (*Neotoma*), the latter solely for the reason that I have previously chosen it as a representative, generalized rodent with which to compare other sorts. But the wood rat belongs to the family Cricetidae of the superfamily Muroidea, while *Dipodomys* is of the superfamily Sciuroidea. Hence it is fitting to use the skull of a squirrel (*Sciurus (Tamiasciurus)*) also in comparison.

Length of skull is a complex factor and can hardly be said to have anything to do with saltatorial habits. Total length of skull can be affected thereby, however, for in *Dipodomys* and other saltators with phenomenal bulla development the mastoid may project for a considerable distance posterior to the condyle. In *Dipodomys* this feature, as well as the long rostrum extending forward of the incisors, increases the total length of skull to the degree where it is about 55 per cent of the body length (the sum of the cervical, thoracic, lumbar and sacral vertebrae), which is very large indeed (*Scirtopoda* 46 per cent, *Allactaga* 48, *Pedetes* 34, *Lepus* 27, *Neotoma* 28). But if condylobasilar, instead of total, length be considered it is found that the percentage in *Dipodomys* is only about 27, and as great as 33 in *Neotoma*. In *Dipodomys* the items which increase the size of the head are relatively light, consisting of a slender muzzle and hollow bullae, so it is probable that its head is no heavier than in some mammals with heads appearing very much smaller.

Width of skull is definitely associated, to various extents, with a high degree of saltation. It is true that an animal may become a great leaper without having a very broad skull (*Allactaga*), but in those with large bullae this feature broadens the posterior part of the skull. Thus in *Dipodomys* the breadth is about 65 per cent of the condylobasilar length, and but 40 per cent in *Neotoma*. As such broadening takes place the eyes must also be placed farther apart, in order that the animal may, to a reasonable degree, watch for an enemy approaching from the rear, and this in turn is accompanied by some broadening of the details immediately anterior to the eyes.

The skull of *Dipodomys* and other rodents with comparable bullae is thus very broad posteriorly, which gives it a triangular appearance. Although it is not particularly deep, relative to length, this is so of

the skulls of certain jerboas and their relatives, in which the bulla development is not phenomenal. This is the case with *Scirtopoda*, and especially *Pedetes*.

It should be noted that in all these rodents the temporal muscles are progressively weaker as saltatorial adaptation advances. Origin of the temporalis freely migrates from the parietal (chiefly) to the squamosal (either exclusively or practically so, as in *Pedetes*), and even to the mastoid part of the bulla, as in *Dipodomys*. In the latter case the temporal muscle is very weak indeed and has probably degenerated (in size) to as great an extent as in any rodent. Undoubtedly in compensation the various divisions of the masseter muscle in these rodents are very well developed indeed. It appears to be the case that in rodents with even moderately large bullae (all those dissected) origin of the styloglossus muscle has migrated from the inferior margin of the auditory meatus in a medial direction almost to the basioccipital border. In addition, the origin of the stylohyoid in *Dipodomys* seems to have migrated from the paroccipital process considerably farther forward. The attachment of these muscles to the bulla is very insecure, however, and it is difficult to define the precise points of origin. The insertion of the cleidomastoid of *Dipodomys* has shifted to a point below the meatus, and of the sternomastoid, definitely anterior to the meatus, which, of course, adds to the leverage of these muscles as compared with conditions in the usual rodent with narrower head, including the jerboas dissected.

Consideration of the position of the foramen magnum together with occipital tilt and the situation of the condyles shows clearly, I think, that the saltatorial rodents under consideration hold the head with the axis tilted downward to a greater degree with respect to the body axis than do the more generalized rodents. In other words the effect of the more erect carriage following the adoption of a partially bipedal mode of locomotion has been accompanied by an appreciable tilting of the head.

For the sake of convenience descriptions of the cranial foramina will be grouped together, preceding presentation of the other cranial elements.

Incisive foramen. This is minute in heteromyids, geomyids, and squirrels. It is enormous (about four times as long) in the wood rat, and intermediate in the jerboas. It is generally presumed that the development of the incisive foramina is correlated with Jacobson's organ, but nothing is known of the reasons for such a disparity in the size of these foramina.

Infraorbital foramen, for the passage of the infraorbital branch of the trigeminal (V) nerve. In murine rodents this is large and V-shaped, between the base of the rostrum and the zygomatic root. In true sciurine rodents it is minute and situated ventrally at the lower part of the zygomatic root. In the jerboas the huge infraorbital fenestration for the passage of a part of the masseter muscle, common to rodents of hystricomorph affinities, is generally termed the infraorbital foramen, but this is incorrect. The true foramen of this name is just as minute as in the squirrels and pierces the maxilla below and at the medial base of the larger fenestration. In all the Heteromyidae and Geomyidae, however, conditions are very different and apparently unique among the Rodentia, for the infraorbital foramen is situated not even adjacent to the zygomatic plate of the maxilla, but upon the side of the rostrum half way between the plate and the incisor. This is a detail which apparently is of great phylogenetic importance. In *Dipodomys* at least the maxillary branch of the trigeminus does not emerge into the orbit as it comes from the Gasserian ganglion as in most other (including sciurine) rodents. It may be seen, from the optic aspect, emerging from the foramen rotundum (practically confluent with the sphenoidal fissure in this animal) but it at once disappears into a canal at the level of the second molariform tooth, and the anterior opening of this canal forms the infraorbital foramen. Hence, in these rodents, the zygomatic plate of the maxilla is pierced by no foramen at all.

There is a foramen in certain rodents which apparently has never received a name. In the jerboas it is situated upon the side of the rostrum at a level with the maxillary root of the zygorama or a bit farther rostrally, somewhat similar but entirely within the orbit of the agouti (*Dasyprocta*), and at the dorsorostral part of the orbit in some heteromyids, but absent as a separate foramen in the wood rat. Dissection shows that it is for the passage of a cutaneous branch of the trigeminus (ramus frontalis) which serves the anterior region of the eye, and it may be known as the *intraorbital foramen*.

Optic foramen, for the passage of the optic nerve (II), is the foramen anterior to the sphenoidal fissure, as usual.

Sphenoidal fissure and foramen rotundum. These are separate in squirrels and the wood rat but combined in heteromyids and jerboas. The former, or anterior lacerated foramen, is for the passage of the oculomotor (III), trochlear (IV), abducent (VI), and first or ophthalmic division of the trigeminal (V) nerves. Through the foramen rotundum when it is present, or otherwise also through

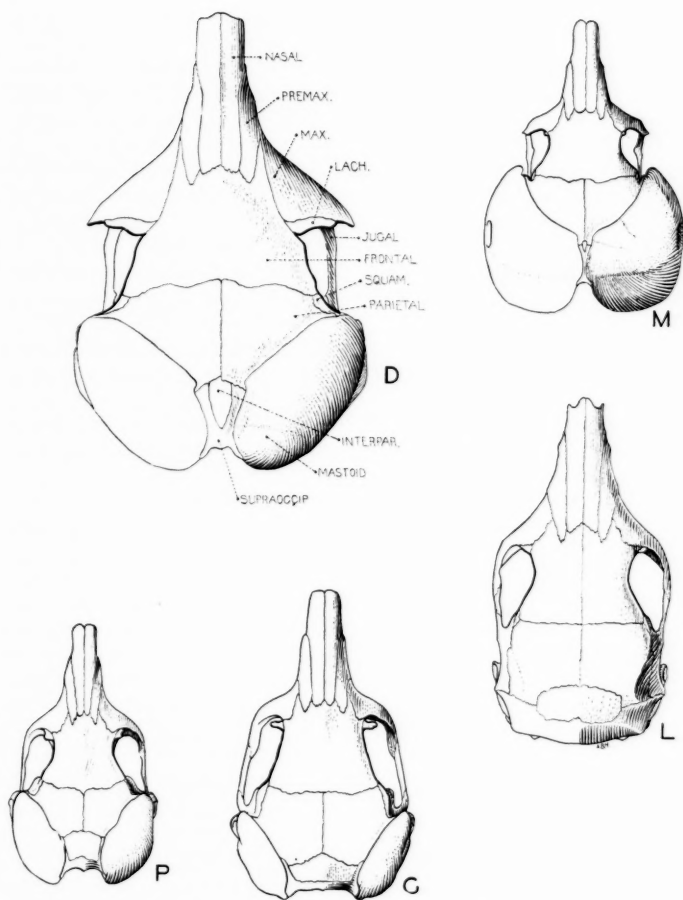


FIGURE 21. Dorsal view ($\times 1\frac{1}{2}$) of the crania of Heteromyidae: *Dipodomys* (D), *Microdipodops* (M), *Liomys* (L), and of the subgenera *Perognathus* (P) and *Chaetopidus* (C) of the genus *Perognathus*. The right half of the skulls is shaded, to show contour, and the left half left blank, to show sutures.

the sphenoidal fissure, passes the maxillary or second division of the trigeminus.

Foramen ovale, for the accommodation of the third or mandibular division of the trigeminus, is present in all examples and pierces the alisphenoid caudal to the foramen rotundum when this occurs.

Pterygoid foramen. Pains-taking dissection is necessary before foramina may be homologized with certainty. For this reason it is unsafe to hazard a statement in regard to just what rodents may or may not have this foramen. It is very possible that in some families or genera it may be confused with an apparent foramen ovale. At any rate the well defined foramen pterygoideus, as represented in the Heteromyidae and Geomyidae by relatively large circular or subcircular vacuities situated between the mesa- and parapterygoid plates, seems clearly to be present in the squirrels, but in smaller form. Careful dissection in three specimens of *Dipodomys* showed that it is for the accommodation of a surprisingly large vein, emerging from between the external and internal pterygoid muscles and extending laterally to the base of the ear, where it joins with the facial and temporal veins to form the external jugular. I was unable to find a trace of the true internal jugular, although readily conceding that a minute one, in an animal of such size, not injected, may possibly have been overlooked. At any rate there is no doubt but that this vein through the pterygoid foramen is the main drain of blood from the brain, and that it has taken over the function of the more usual internal jugular vera. The true homology of what may be called this pterygoid vein is unknown. Certainly it seems to be entirely unrepresented in most mammals, including the cat, but in primitive Mammalia it may possibly occur as a small vessel and this, if of aid in draining the blood sinuses at the base of the brain (as inferior petrosal or cavernous sinuses) could easily, if the need arose, develop to assume the entire duty of a true internal jugular.

Middle lacerated foramen is variable in size but occurs as a rather large, irregular vacuity in *Dipodomys*, larger still in *Sciurtopoda* and *Dipus*, and as an enormous, elongated one in *Allactaga*, between the alisphenoid and audital bulla. It seems that this is chiefly a vacuity. It is much larger than needful for the passage of small nerves and blood vessels even in *Dipodomys*, in which it was ascertained that the carotid artery does not enter the endocranium at this point, although it very probably does so in the jerboas, as in most other mammals.

Stylomastoid foramen, for the passage of the facial (VII) nerve. This is located immediately caudal to the auditory meatus, between

the mastoid and audital bullae in most mammals, slightly ventral to the level of the meatus in the jerboas, and relatively far below it in heteromyids. In the more specialized of the latter it is useful in locating the junction of the petrous and tympanic portions of the temporal complex.

Posterior lacerated foramen. In the rodents examined this varied from an aggregation of several irregular foramina to a rather broad, slit-like vacuity between the basioccipital and the audital bulla. The latter is the condition in *Dipodomys*. In this genus it was found not only that there was no internal jugular, as already mentioned, but that the point of entry to the endocranium of the internal carotid had shifted, possibly as an accompaniment of bulla development, so that it entered through the rostral part of the posterior lacerated foramen. Emerging caudal to this artery were the glossopharyngeal (IX), vagus (X), and spinal accessory (XI) nerves. Presumably these conditions are the same in the other heteromyids but probably not in the jerboas, sufficient specimens of which were not available to determine all such points.

Stapedial foramen. This foramen, heretofore unnamed, is so termed for the reason that it accommodates the stapedial artery, which occurs in many mammals, but in man only until the third month of fetal life. In the species considered in the present connection it was absent only in *Liomys* and *Thomomys*, but its usual situation in nonheteromyids is farther caudalward near the paroccipital process. In rodents having this foramen it will be found that the internal branch of the carotid splits in the vicinity of the basioccipital into two arteries of approximately equal size. One of these becomes the true internal carotid and the other the stapedial artery, piercing the bulla near the basioccipital (fig. 26) and passing through the stapes.

Squamosal foramen (fig. 25). This is a foramen of generous size that pierces the squamosal of *Dipodomys* and is visible within the orbit from an obliquely anterior aspect. Dissection upon both sides of a spirit specimen, with this detail especially in view, showed that it is for the passage of a blood vessel. No nerve was here detected.

Condylloid foramen, for the passage of the hypoglossal (XII) nerve, is present in all skulls examined, but is especially small in heteromyids and jerboas. In *Allactaga* it is double. It occupies its usual situation ventrolateral to the condyle.

In addition to the foramen magnum and those mentioned, there are, of course, many small foramina in the skull for the passage of small blood vessels and nerve filaments. In certain forms some of

these may ultimately prove to be of great importance but their proper treatment depends upon lengthy research.

Nasals. The shape of the nasals is influenced by the conformation of the snout proper and of the rostrum as a whole. In the Heteromyidae both of these features depart widely from cricetine and sciurine conditions. In heteromyids the snout is elongated and hence the nasals project well beyond the incisors, to as great an extent in *Dipodomys* as 4 mm., and are inclined to be tubular distally, each one in cross section describing about one third of a 4 mm. circle. The latter feature is most pronounced in *Microdipodops*. This character of projecting nasals is not shared by geomyids, with their short nose. Neither are the nasals definitely elongated in jerboas of the genera *Allactaga* and *Scirtopoda*, but there is some elongation encountered in *Salpingotus*, with its enormous bullae.

Premaxillae. The anteriormost portion of these bones in the Heteromyidae is prolonged into a distinct process upon each, which projects considerably beyond the vertical situation of the incisors to join the anterior thrust of the nasals. Thence they descend and join to form the U-shaped floor of the anterior nares, and thence descend still farther for a considerable distance to form a sharp, vertical, median ridge between the incisors. This is not the case in the wood rat, squirrel, or pocket gopher, but a somewhat similar situation prevails in the jerboas, especially *Scirtopoda*, in which the premaxillae ensheath the incisors more pronouncedly. In other respects these bones, in all the rodents here considered, conform to the same general plan. The ascending branches always extend posterior to the nasals, and the extent of their lateral areas conforms more strictly to the relative size of the skull than to relative length of rostrum. In other words the lateral area of the premaxilla is somewhat the same in an animal with long rostrum as in one having this feature much shorter. In the latter sort the maxilla is the detail which suffers reduction. The lateral area of the premaxilla is, however, affected in the Heteromyidae by the peculiar situation of the infraorbital foramen, for the premaxillo-maxillary suture always passes rostral to this foramen. The incisive foramina of the Heteromyidae are of the minute, sciurine type and they are bordered practically entirely by the premaxillae. In the jerboas, as in the wood rat, these foramina are much longer and the premaxillae and maxillae are about equally concerned. Toward the terminations of the ascending branches of the premaxillae of heteromyids there are no extremely small "nutrient" foramina such as are present in varying number in geomyids.

For the Geomyidae, Merriam (1895) has described an internal narial detail which he termed internal vertical plate of the maxilla. Its analogue is present in *Dipodomys* but in this animal the premaxillo-

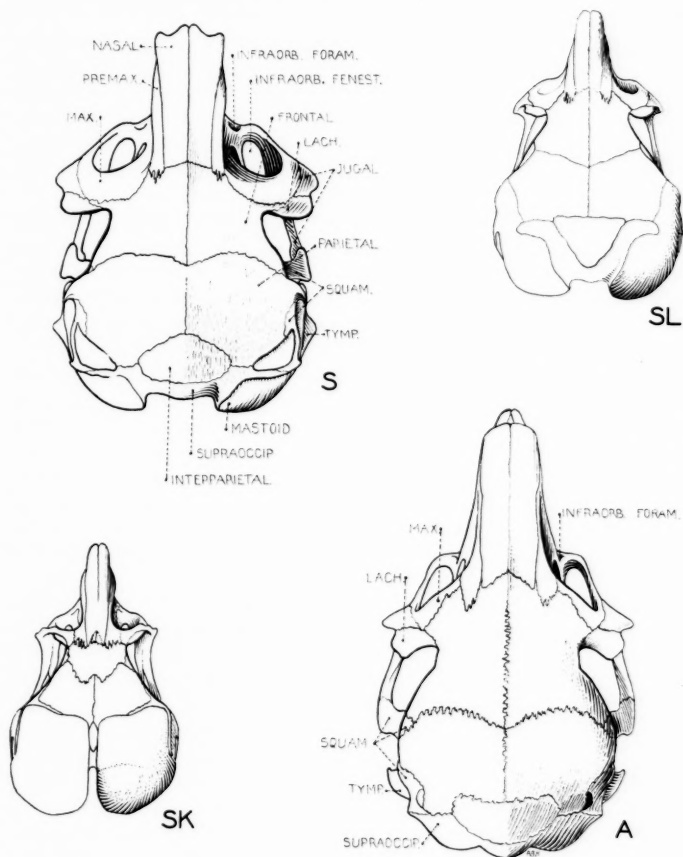


FIGURE 22. Dorsal view ($\times 1\frac{1}{2}$) of the crania of Dipodidae: *Scirtopoda orientalis* (S), *Scirtopoda lichtensteini* (SL, redrawn from Vinogradov), *Salpingotus kozlovi* (SK, redrawn from Vinogradov), and *Allactaga* (A).

maxillary suture is located farther forward in respect to the incisive foramina than in the pocket gopher. Presumably in correlation with this is the fact that in the kangaroo rat the internal vertical plate, in the form of a lamina arising lateral to the vomer, is formed by the premaxilla.

Maxillae. The maxillaries are largely affected not only by rostral features but by any peculiarities that may occur in either the anterior brain case or zygomatic arches. In the Heteromyidae they are altered by the character of the infraorbital foramina, and in *Dipodomys* especially by the broadness of the prezygomatic features, but the latter are not altogether an accompaniment of bulla development, for this is not pronounced in *Microdipodops*.

As already described, the infraorbital foramen is extremely variable in these major groups of rodents. In murine and cricetine types it is V-shaped and situated dorsally between the zygomatic plate and the rostrum. In sciuriforms it is minute and circular, near the ventral border of the zygomatic plate, close to the dental arch and usually if not always subtended by a pronounced process for the attachment of the superficial masseter muscle. In hystricomorph types, including the jerboas, it is also minute, but maxillary conditions are complicated by the situation above it of the huge infraorbital vacuity, for the passage of a part of the masseter muscle. In heteromyids and geomyids it is situated far cranialward upon the rostrum. The resulting conditions are more clearly shown by the illustrations than verbal descriptions. Usually in these rodents the infraorbital foramen is bounded completely by the maxilla but occasionally the premaxilla borders it anteriorly.

Of great influence in contributing to the characteristic appearance of the skull of *Dipodomys* is the broad, flaring, superior part of the maxillary zygomatic root. In the less specialized of the heteromyids this is no more pronounced than in the average squirrel, and this is also largely the case in *Microdipodops*, so the character is not necessarily correlated with increased width of skull because of bulla development, but rather does it seem to have been caused partly by orbital requirements, perhaps, and largely because of muscular needs. It should be mentioned that in the wood rat and similar murines and cricetines, the form of the infraorbital foramen and cavernous character of the bone within this renders it unlikely that any distinct maxillary sinus occurs. In the squirrel, pocket gopher, and heteromyids, however, this sinus is large and well formed, being especially extensive in the last group, partly as an accompaniment of the small

incisor root. In *Dipodomys* it invades the maxillary root of the zygoma for some distance.

In heteromyids the relation of the zygomatic root of the maxilla to the jugal is not much different from the condition in the wood rat, but in the jerboas, because of the infraorbital vacuity, it is of another pattern and completely surrounds the vacuity. In *Salpingotus* the ventro-caudal termination of the zygomatic root is prolonged caudward by means of a long process (fig. 24).

Jugals. In the pocket mice examined this bone is of the general type of that of the wood rat, but more slender and occupies the posterior half or three-fifths of the zygomatic arch. In the squirrel it is laminated over the maxillary root and reaches the lachrymal, while in *Dipodomys* and *Microdipodops* it is intermediate between these two conditions, partly overlapping the expanded portion of the maxillary root with the slight expansion more horizontal than vertical. At a point in *Dipodomys* about 4 mm. from the posterior termination there is a sharp spinous process upon the medial aspect, barely indicated in *Microdipodops*. In the jerboas this bone also reaches the lachrymal, is very extensive indeed, and of a right-angular shape, because of the conformation of the infraorbital vacuity. In *Scirtopoda* especially the anterior part is expanded in a posterior direction, which is not pronounced in *Allactaga* nor *Salpingotus*.

Lachrymals. This bone is invariably present, flush with the bony surface in the squirrel but it is more in the nature of a process in the others, and somewhat broader and strap-shaped in the jerboas and *Dipodomys*. The mediorostral border articulates with the maxilla except in *Perognathus* and *Microdipodops*, in which genera it takes the form of a relatively long process, chiefly from the frontal, and is particularly apt to be lost during cleaning of the skull. The squirrel appears to be the only one of these rodents in which the lachrymal canal pierces this bone. In the wood rat the bony canal seems to be absent, the duct passing within the infraorbital foramen and so to the nasal passage through a vacuity in the bone. Neither does a foramen occur in *Scirtopoda* and the route of the duct is not apparent. In *Allactaga* a foramen, evidently for this duct, is found in the frontal nearby, while in the Heteromyidae it pierces the maxilla just below the lachrymal.

Vomer. In rodents with narrow rostrum the internal details of this part of the internal nares are much compressed laterally. The vomer of *Dipodomys* is exceedingly thin but quite extensive vertically. It rests upon the floor of the nasal cavity between the internal vertical

plates of the premaxillae and divides above, forming two ascending wings which closely clasp the mesethmoid cartilage. The bone thence (caudalward) arises from the floor of the nasal passage to extend in a slender process which ends at the base of the cribriform plate.

Palatines. The palatal bones of *Dipodomys* unite with one another at an early age, and frequently, at a later stage, with the maxillae and other adjacent bones as well. They form the ventral and lateral borders of the posterior nares and the extreme anterior part of the pterygoid fossae and are considerably different in conformation from conditions in the wood rat. A medial palatal spine, posteriorly directed, may be present or absent but is frequently very long (3 mm.) in *Dipodomys*. The precise position of the posterior nares in relation to the last molar is variable, being situated more rostrally in the wood rat, intermediate in *Dipodomys*, and farther caudalward in the squirrel and jerboas.

Ethmoids. Filling the rostral part of each half of the nasal cavity are the nasoturbinal and maxilloturbinal. The former is attached to the extreme lateral border of the nasal bone and its ventral part is grooved for receiving the border of the maxilloturbinal. The latter is more nearly horizontal, and parallel to the nasoturbinal, than seems to be usual in rodents. It continues rostrally from the maxilla upon the dorsorostral border of the infraorbital foramen, but its anchorage within the nasal passage seems to be more concerned with the premaxilla than the maxilla.

The remainder of the ethmoid complex in *Dipodomys* consists of mesethmoid, cribriform plate, and ethmoturbinals. The sagittally situated mesethmoid bone is rather short, but the mesethmoid cartilage extends therefrom almost to the anterior nares. Caudally the osseous connection is with the cribriform plate, and dorsally with the anterior part of the frontal shield. The cribriform plate, forming the rostral wall of the brain case, is, if anything, a trifle larger than in the wood rat. The perforations for the olfactory filaments are very numerous indeed and the cerebral surface is finely crenulated, to correspond with the turbinal folds, but this is much less marked in other rodents examined.

The fragile convolutions of the ethmoturbinals are bounded caudally by the cribriform plate, medially by the mesethmoid, and laterorostrally by the medial wall of the maxillary sinus, except that the latter does not join the mesethmoid rostrally, leaving a slit which constitutes the olfactory and respiratory parts of the nasal passage. Within this

bony capsule the ethmoturbinals are expanded dorsally and more constricted ventrally.

Frontals. A character exhibited strongly by the pocket gopher is the tendency for the early obliteration of the suture between the

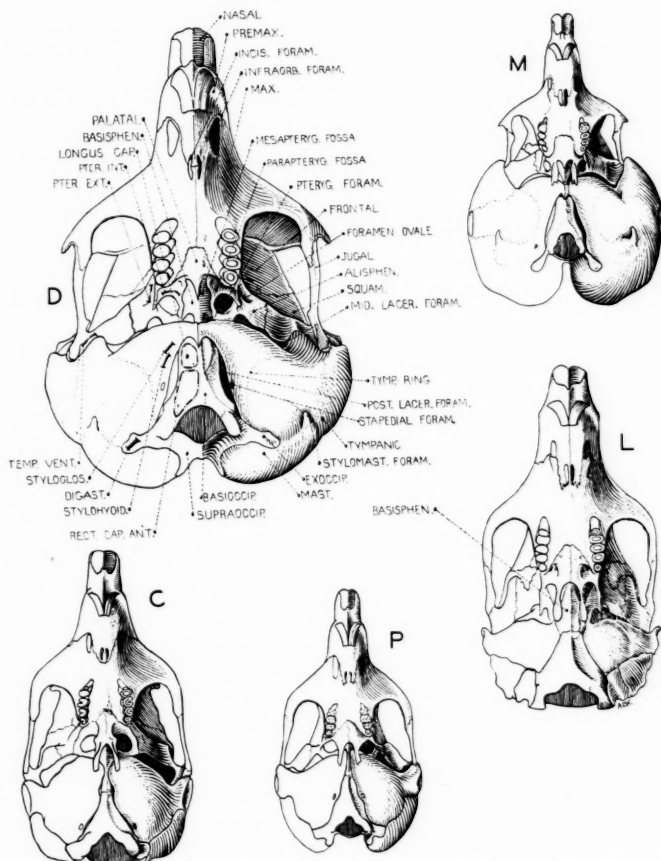


FIGURE 23. Ventral view ($\times 1\frac{1}{2}$) of the crania of Heteromyidae: *Dipodomys* (D), *Microdipodops* (M), *Liomys* (L), and of the subgenera *Chaetodipus* (C) and *Perognathus* (P) of the genus *Perognathus*.

frontals. Hence, this character encountered in *Dipodomys*, but less strongly marked, can hardly be correlated with the breadth and flatness of this part of the skull. In the wood rat the frontals are very narrow, considerably broader in the squirrel and the jerboas, and exceedingly broad in *Dipodomys*; but this character is less pronounced in other heteromyids, including *Microdipodops*. Whereas in most rodents the frontals are thin and fragile, in the majority of heteromyids they are thicker, with characteristic cancellous tissue internally and smooth, fine-grained plates upon the ental and ectal surfaces. This is most pronounced in *Dipodomys* and it is apparent that strength is thereby added as the skull becomes broader and flatter. But the reason why *Microdipodops* should lack this character is obscure.

In *Dipodomys* the frontal bones have the general form of a vertical section through a truncated cone. This frontal shield is very broad posteriorly, and regular except at the anterior boundary, which conforms in outline to the irregularities caused by the posterior terminations of the nasals and ascending branches of the premaxillae. An acute, anterior process is also projected upon each side between these ascending branches and the maxillary plates of the zygomatic arches. The angle formed by the frontal shield with its orbital plate is acute and sharp. This plate extends caudalward from the lachrymal, the anterior suture being with this bone and the maxilla, the inferior one with the orbitosphenoid, and the posterior with the squamosal; but the ossification of the inferior portion and of the adjoining orbitosphenoid is incomplete and their precise boundaries in this region are indeterminable.

Sphenoids. The precise limits of the basi-, ali-, orbito-, and presphenoids are not easy of determination in *Dipodomys*, for they appear to be fused completely. The most important details, from the present standpoint, occur in the pterygoid region. In heteromyids and geomyids this is very characteristic, with foramina passing endocranially, one in either pterygoid fossa. The anterior part of the latter is shallower than in the jerboas but deeper than in either the wood rat or squirrel, and in all they extend farther rostrally, as compared with the mesopterygoid fossa, than in the wood rat. In adult skulls of none of these rodents are there separate pterygoid bones but these occur in *Dipodomys* of tender age, and doubtless in comparable skulls of the others as well. It should be mentioned that the choanae or posterior narial opening is more restricted in *Dipodomys* and *Microdipodops* than in the others.

In *Dipodomys* the orbitosphenoid is very fragile and there is usually,

if not always, an irregular vacuity between it and the frontal with ossification incomplete. From the endocranial aspect it is seen that the optic foramen is almost as large as the sphenoidal fissure, and that the presence of the pterygoid foramen and foramen ovale are instrumental in forming, endocranially, a strong, bold, alisphenoid bridge between the former and the middle lacerated foramen.

In the jerboas the orbitosphenoid is largely the same save that the vacuity occurs between this bone and the squamosal. In all of them the sphenoidal fissure is combined with the foramen rotundum and is situated between the orbito- and alisphenoid.

In all of them also the alisphenoid is prominent and constitutes an irregular ridge between the palatal and squamosal. This bone forms most of the parapterygoid plate and is pierced by the foramen ovale.

The basi- and presphenoids are fused, but from an examination of an immature skull of *Dipodomys* it is seen that the former constitutes that part of the bone dorsal to the junction of the horns of the bullae and as far rostral as the level of the pterygoid foramen, while the presphenoid, from the endocranial aspect, ends just short of the cribriform plate. It is not quite so narrow and rod-like as in the jerboas.

Parietals. The tendency in the Heteromyidae is for the parietals to adopt a rectangular shape and without rostro-lateral extension as in so many other rodents (wood rat, squirrel, and even the pocket gopher). Thus the parietal-frontal sutures together form an essentially straight, transverse line, characteristic in less marked form also of the jerboas examined. The outline of the laterocaudal part of the parietal, however, is modified in direct ratio to the development of the bulla, at first slightly so in the pocket mice, and greatly so in the kangaroo rats and mice, becoming almost completely triangular in such forms as *Dipodomys deserti* and *Microdipodops*. In these animals the modification is such that only an exceedingly restricted part of the parietal border is adjoined by the squamosal; and the encroachment of the enormous bullae upon the midline has all but eliminated the parietal-supraoccipital sutures.

In *Allactaga* the parietal-frontal, parietal-parietal, and parietal-interparietal, as well as the frontal-frontal, sutures are of an exaggeratedly dentate type that must be particularly strong, but this character is shared by none of the other species under consideration.

Whereas in heteromyids the reduction of a part of the parietal accompanying bulla development gives the appearance of having been accomplished by a simple horizontal crowding of the bulla, in

the jerboas this is not the case. Clearly in these animals the course of development has been in the nature of first the enlargement of the bullae beneath the parietals, as well as the squamosals and occipital, and later the partial atrophy of the portions of these bones so affected.

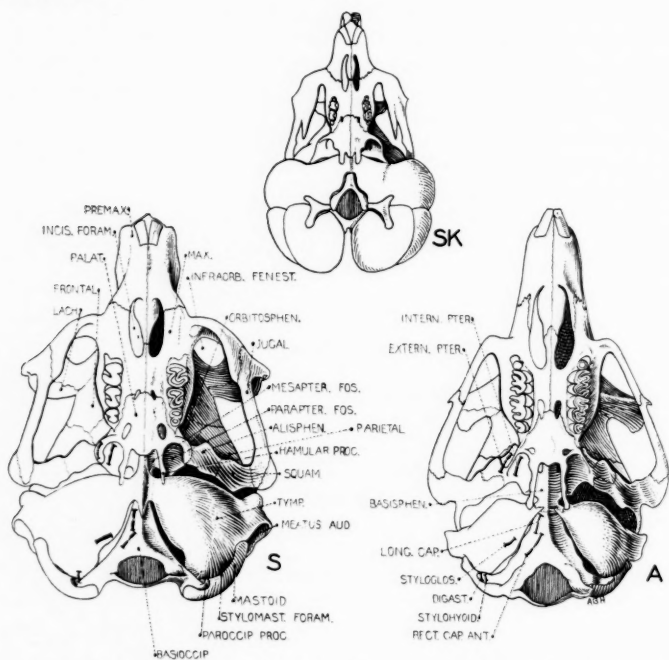


FIGURE 24. Ventral view ($\times 1\frac{1}{2}$) of the crania of Dipodidae: *Scirtopoda orientalis* (S), *Salpingotus kozlovi* (SK, redrawn from Vinogradov), and *Allactaga* (A).

Interparietal. It is difficult to escape the conclusion that in the majority of mammals at least the character of the interparietal is definitely correlated with the development of the temporal fossae. The enlargement of the temporal muscles to the point where there is a sagittal crest, will usually not only be accompanied by reduction of the interparietal, but also by fusion of this element with the parietals

and elimination of the sutures involved. Similarly, as a rule, the broadest interparietals are often encountered in mammals having the weakest temporal muscles. *Dipodomys* forms an interesting exception to this, reduction of the interparietal having been clearly brought about by enlargement of the audital bullae.

In the pocket mice the tendency is for this bone to be rectangular, and considerably greater in transverse than in sagittal dimension save in those forms with bullae that are larger than usual (as *Perognathus amplus*). In the majority of kangaroo rats (as *Dipodomys spectabilis*) the interparietal is narrow and shield-shaped, bounded laterally by the ascending branches of the supraoccipital. In *Microdipodops*, with its enormous bullae, this bone is a minute vestige, and in *Dipodomys deserti*, whose bullae approach one another to a greater degree than any other species of the genus, the interparietal seems to have been crowded out completely.

In the jerboas the interparietal is well defined but with nothing distinctive. It may be broadest either cranially or caudally.

Temporals. This part of the skull, consisting of squamous, petromastoid, and tympanic or audital portions, is of the usual complexity.

In the less specialized of the *Heteromyidae* the squamosal is not markedly different from that encountered in such rodents as the wood rat or the squirrel. Seemingly of chief interest is the conformation of the part of the bone about the mastoid process of the squamosal, in so many rodents bordering the prelamdboidal fenestration of this bone. In neither heteromyids, geomyids, nor jerboas is this fenestration present, although in *Allactaga* there does occur a small vacuity between the squamosal and parietal.

In *Liomys* a process of the squamosal which doubtless represents the mastoid process forms the superior lip of the auditory meatus, but in the specimens of *Perognathus* (of both subgenera) examined this process occurs above the meatus and is long and very slender. In *Dipodomys* and *Microdipodops* it is clearly indicated above the zygomatic root of the squamosal, although in these genera it does not extend caudally anywhere near the meatus. It is interesting to note that this process is more conservative than the part of the squamosal which in more generalized rodents usually articulates with the occipital just above the fenestration.

As the bulla develops the more ventral part of the squamosal is also affected, to the extent where the bulla directly adjoins or even overlaps laterocranially the glenoid cavity (*Microdipodops*). In the more specialized sorts the zygomatic process of the squamosal is

extremely short—a condition likely correlated with the great width of the posterior part of the skull, as it is a character shared with the jerboas.

It should be noted that in *Dipodomys spectabilis* there is a ridge or shelf visible in ventral aspect between the glenoid cavity and the zygomatic process, marking the attachment of an interesting and peculiar muscle slip, tentatively termed the ventral slip of the temporal. This ridge, and apparently the muscle in well marked form, is absent in *D. deserti* and this difference serves to differentiate adults of the two species at a glance without recourse to other characters.

In the jerboas the termination of the zygomatic process of the squamosal is notably robust but in other respects the ventral aspect of this bone is not noteworthy.

In many mammals the petrosal and mastoid portions of the temporal are so well fused that it is entirely impracticable to define their precise junctions. In those of the character of the wood rat and squirrel, however, as in most other sorts, it is at least easy to differentiate externally between the tympanic bulla and the mastoid, partly by the difference in the texture of the bone and always by the situation of the mastoid between the lateral or ventral part of the lambdoidal crest, the exoccipital, and the tympanic bulla. But it is hardly possible to distinguish between the mastoid and petrous portions of the temporal save in a general sense.

It may be said that both the mastoid and the tympanic bulla in the wood rat and the squirrel are of moderate size, the former with a flat surface and the latter subspherical in form with a fair degree of inflation. In both there is a faint indication of a projecting lip to the auditory meatus.

As the pocket gophers (Geomyidae) are more closely related to heteromyids than are any other living mammals it might be expected that these would show some tympanic resemblance to the conditions in *Dipodomys*. This is not the case and it appears likely that in this detail the two groups have followed opposite courses of development. But if the more generalized members of the Heteromyidae are compared both with *Thomomys* and *Dipodomys* various similarities may be noted. In the former the bulla is flatter than in the average murine rodent and is projected into a flask-like meatus that is relatively of very small diameter. This character of tubular meatus is met in varying degree in the less saltatorial of the heteromyids, apparently occurring in inverse ratio to bulla size. It is present in fair degree in *Liomys irroratus* and to a progressively lesser extent

through the hairy and then the silky pocket mice to the kangaroo rats and mice, in which the meatus is of large diameter and is flush with the globular surface of the bulla.

In this connection there should be mentioned the situation as reported in *Liomys canus*, by Allen (1904). It appears that in this species there is a small, semitubular ossicle at the base of the ear cartilage which is hinged to the lip of the meatus by a ligamentous structure. That this is a development for fulfilling some definite audital function is indicated by its presence in other rodents of both Old and New Worlds (*Ctenodactylus*, *Pectinator*, *Chinchilla*). As the cartilage of the auricula is considered to be phylogenetically a continuation of the hyoid complex it would not be particularly surprising to find an occasional auricular center of ossification. I have failed to find it, however, in several species of *Perognathus*.

In *Liomys* the mastoid and body of the audital bulla are both very similar to conditions in *Thomomys* save that the former is relatively a bit larger. The transition from this stage to the extreme situation in *Dipodomys* is then perfectly illustrated by examining successively *Perognathus* (*Chaetodipus*) *baileyi* and *P. (P.) amplus*. It will be seen that this is accomplished by extreme enlargement of the mastoid accompanied by a much slighter increase in the size of the audital bulla. The course of procedure is for the visible part of the mastoid to increase first dorsally, and then both rostrally and medially. The exoccipital is at first not as much affected as the supraoccipital, which is crowded medialward, and the part of the squamosal above the meatus, which is practically eliminated as the mastoid replaces it. At a later stage (*Perognathus amplus*) the conformation of both ex- and supraoccipital is much affected by crowding of the mastoid, as are both interparietal and parietal. While this change in the mastoid is taking place the visible portion of the audital bulla is altered in but slight degree, relatively speaking. There is some increase of inflation and rostral extension of the anterior cornu to the midline of the posterior interpterygoid fossa. Finally, when a skull of *Microdipodops*, or even *Dipodomys*, is examined, one can not fail to gain the impression that the entire nonsquamous portion of the temporal has developed as a single unit to a single end, and the result is a relatively huge, bulbous structure that has distorted the entire caudal part of the skull.

From an examination of the skulls of *Dipus*, *Sciurtopoda* and *Allactaga* at hand it seems clearly indicated that the enlargement of the bulla of the jerboas has followed a somewhat different procedure.

In these the inflation of the audital bulla is more pronounced than in any heteromyid, although in *Allactaga* the cornua are not projected to the midline. In *Allactaga* the mastoid is very small, considerably larger and quite well inflated in *Dipus*, and more pronouncedly so in *Scirtopoda*, the mastoid being about as capacious as the audital bulla. Illustrations of *Salpingotus* seem to indicate that thereafter, in the saltatorial specialization of the acoustic apparatus in jerboas, the audital bulla increases but slightly in size while the mastoid experiences inflation surpassing in degree even the kangaroo mice. The association in this group of the zygomatic root of the squamosal with the audital bulla is much less intimate than in heteromyids.

In *Pedestes* there is still another trend, for its audital bullae are perhaps relatively smaller than in the average rodent, while the mastoids are very large indeed.

By an examination of the external surface of the *Dipodomys* bulla one can distinguish certain landmarks. Thus, in the area between the posterior border of the meatus and the exoccipital process is a faintly defined sulcus, marking the junction of the audital and mastoid portions of the bulla; and along this sulcus is situated the stylomastoid foramen for the passage of the facial nerve. Bordering the foramen is a projection of bone, flush with the surface, that is apparently the homologue of a mastoid process of the usual character. Extending forward from the superior border of the meatus is another irregular line, marking the junction of the mastoid and audital portions. A third sulcus extends from the posterior border of the meatus dorsally and then medially to the vicinity of the posterior part of the interparietal, marking the position of a septum which divides the mastoid into medial and lateral chambers. By close attention it is usually possible to distinguish externally the arc of the tympanic ring, occurring, in ventral aspect, about half way between the pterygoid fossa and the stylomastoid foramen. It usually takes the form of a whitish, curved line and its conformation in *Dipodomys* shows that the tympanic membrane is tilted at an angle about half way between vertical and horizontal. In the squirrel, wood rat and the jerboas it is more nearly vertical. The only other foramen which may be distinguished externally is that for the passage of the stapedia artery, piercing that part of the bulla adjacent to the basioccipital.

By removing the parietals and a part of the frontals from a skull of *Dipodomys* the medial aspect of the auditory complex is exposed. By gross comparison of the details of this animal with those of a wood rat and a cat, it is seen that the tentorium, separating the cerebral

from the cerebellar part of the brain-case, is derived in the cat entirely from the parietal. In the wood rat the latter bone plays no part in the formation of the tentorial process but this is derived from both mastoid and petrosal elements, and this is the case in *Dipodomys*. This detail, however, cannot be settled with certainty in the case of the single skull of *Scirtopoda* which was dissected; but it appears likely that both parietal and auditory elements are involved, and that in different mammals the derivation of the tentorium may vary with other details.

The medial aspect of the auditory apparatus is suggestive that this item has both modified and been modified by the conformation of the brain. There is a broad, bony depression between the tentorium and the squamosal to accommodate the occipital pole of the cerebrum, and this is of rather uniform curvature.

The infratentorial part of the ear bone can be examined only after separation of this portion from the remainder of the skull. When this has been done it is seen that the depression between the tentorium and supraoccipital is broken up into a superior fossa that is shallow and rather broad, for the accommodation of the anseriform and paramedial lobules of the cerebellum, and a smaller inferior fossa, much deeper, into which fits the paraflocculus.

Upon this aspect the tentorium passes ventrally and rostromedially along the tympanic cornu practically to the tip of the latter, which articulates with its fellow of the opposite side. Near its anterior termination the tentorium is thrown into a fold, bridging a large foramen for the passage of the semilunar or Gasserian ganglion of the trigeminus (N. V). Upon the apex of the tympanic cornu is the foramen for the passage of the Eustachean tube.

The ventral part of the supratentorial depression is pierced by a foramen for the emergence of the stapedia artery, which then occupies a sulcus in the bone for some distance rostrally. Investigation discloses the course of this artery through the tympanic structures to be entirely within a bony canal, extending from the neighborhood of the basioccipital as before stated, skirting a part of the rim of the fenestra rotunda at the base of the cochlea, and passing between the crura of the stapes before emerging upon the supratentorial depression.

Rostromedial of the parafloccular fossa there are (in the infratentorial area) two foramina of considerable size, within which one may distinguish branches and cribriform spots. The more dorsal of these foramina accommodates the facial nerve (N. VII), and through them pass the cochlear and vestibular branches of the acoustic nerve (N.

VIII). Effort, expended upon several specimens, both cleaned and in spirits, to follow the nerve passages involved was only partially successful, and it is only after histological study of the skull that the

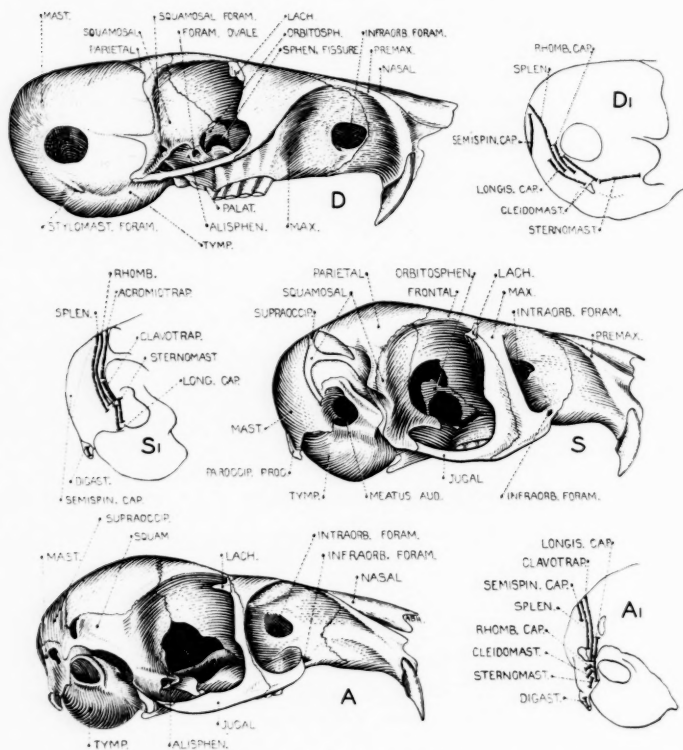


FIGURE 25. Lateral view of the skulls of *Dipodomys* (D), *Sciutopoda* (S), and *Allactaga* (A), showing also the areas of attachment of some of the cervical muscles.

topography of the finer nerve twigs of the inner ear can be determined with exactitude.

As already mentioned the dorsal and caudal parts of the bulla of *Dipodomys* are composed entirely of mastoid elements, which are

separated from the tympanic portion of the bulla by a bony septum. The latter passes from the zygomatic root of the squamosal caudally along the superior border of the external auditory lumen and thence ventrally to the stylomastoid foramen. From this point two irregularly semicircular lines diverge to join at the exoccipital process and the small area thus inclosed (fig. 26) marks a portion of the mastoid which has overthrust the tympanic, thus forming a small, superficial sinus. The mastoid is entirely cavernous and is divided into a dorsal and a posterior sinus by a thin, bony septum which extends from the posterior border of the external auditory passage to the region of the interparietal.

The dorsal mastoid sinus is a large chamber whose fragile dorsal boundary is strengthened rostrally and medially by bony buttresses. The medial wall is dihedral, the anterior marking the cerebral and the posterior the cerebellar part of the septum. The sinus communicates with the entotympanic cavity (middle ear) by a ventral fenestration through which may be seen the malleus and incus. On the lateral border of this fenestration is a process, upon the summit of which is a minute foramen, for the passage of the ligament of the tensor tympani muscle. Upon the anterior border of the fenestration the rounded margin gives the appearance of being tubular, but it has no lumen and hence would seem to be rod-like for strength. In the more caudal part of the sinus the most striking feature is a portion of the superior semicircular canal, with its ampulla, and below it, the less well marked rostromedial portion of the lateral canal.

The posterior mastoid sinus is smaller than the dorsal, is rectangular in shape and extends dorsomedially. Its walls lack buttresses. Ventrally it also communicates with the entotympanic cavity by means of a fenestration. The most conspicuous features are the extensive curvatures of the posterior and lateral semicircular canals. From the middle of each of these, as well as from the ventral part of the posterior canal, extend bony struts with rounded margins. The fenestration is bounded by the two most lateral of these three struts, and between them is visible the stapedial canal. Lateral to the fenestration and extending from the vicinity of the lateral semicircular canal is the curvature of the bony canal transmitting the facial nerve, which is, in reality, within the lamination between the posterior mastoid sinus and the tympanic. Just lateral to the base of the canal, from the posterior aspect, is a smaller, accessory fenestration communicating with the fossa incudis of the entotympanic.

The true part that the mastoid element plays in the scheme of the temporal complex has never been determined. Certainly by medical men and in all probability by comparative anatomists as well the mastoid is usually thought to be a part of the skull posterior to the ear, composed internally of cancellous or multicavernous tissue which in man may become distressingly infected. Certainly the story of the mastoid cannot be told on a part of one page, but it may be permissible here to point out that in many mammals having use for an efficient balancing organ in the form of a large tail, such as the wood rat for one, the hard, thin shell of the mastoid is completely filled by the bulbous paraflocculus of the cerebellum. Although there may well be exceptions, on the whole it seems safe to say that only following the relative increase in the size of the mastoid element (*Perognathus*) or decrease in the paraflocculus in such mammals as do not employ a long tail for balancing or some such use (pocket gopher, man) does the mastoid take on a markedly cancellous character, the individual cells of which probably communicate with the middle ear. And in the former eventuality the cancellous character of the mastoid becomes lost following extreme hypertrophy (kangaroo rat), or in some mammals (jerboas) even moderate enlargement, of this element.

An examination of other available Heteromyidae indicates the successive steps probably followed during the development of the *Dipodomys* mastoid. In *Liomys* (as in geomyids) the small mastoid is composed of cancellous bone whose airspaces are all of small size. In *Perognathus baileyi* there is a thick surface area of more fragile, finely cancellous tissue with a deep sinus of considerable size. In *P. amplus*, with its larger mastoid, the cancellous zone is thinner while the deep sinus is larger, although still single. In other species of *Dipodomys* and in *Microdipodops* the individual details vary to some extent but not to an important degree.

In the jerboas it was found that the mastoid of *Allactaga* was, on the whole, very similar in size and general conformation to that of *Liomys*, save that there was quite a large fenestration. This opened within a mastoid that had no sign of cancellous tissue but which was hollow and with an outer wall that was very thin, much as in the wood rat. The mastoid shell thus formed communicated with the endocranium and was completely occupied by a paraflocculus with a constricted base. In *Dipus sowerbyi* the slightly smaller parafloccular fossa was comparable to the extent that it was located within a hollow mastoid, but there was no fenestration communicating with

the ectal surface, and only a part of the mastoid was thus occupied. This was the extreme caudomedial part, adjoining the occipital. The more lateral and rostral part of the mastoid, located above and immediately behind the auditory tube, was thin-walled and cavernous, and was separated from the parafloccular diverticulum of the mastoid by a thin septum. This large sinus communicated, in the cleaned skull, with the ectotympanic vestibule, by a circular vacuity situated immediately dorsal to the tympanic membrane. Across this foramen, in the spirit specimen of *Scirtopoda*, there was stretched a delicate, transparent membrane very comparable to a tympanic membrane. It is thus indicated that both *Scirtopoda* and *Dipus*, and probably other specialized genera of jerboas, are equipped with a resonantly cavernous mastoid whose efficiency is augmented by a membrane between it and the ectotympanic vestibule, while in *Dipodomys* the larger mastoid opens into the middle ear.

In *Scirtopoda* the development of the mastoid has been carried still farther than in *Dipus*, chiefly dorsally and to some extent caudally, so that the parafloccular diverticulum is over-ridden (from the lateral side in a caudomedial direction) by the mastoid sinus proper. The latter develops two buttresses, comparable to those in *Dipodomys* but more extensive, which almost separate the mastoid into anterior, middle or dorsal, and posterior sinuses.

In many mammals, as the Carnivora, Insectivora, etc., the tympanic part of the temporal complex is derived from an external ectotympanic annulus, of varying robustness and extent, chiefly for supporting the tympanic membrane, and an entotympanic portion, comprising the remainder of the audital bulla proper. It is the rule for these two elements eventually to fuse, and at times this occurs at a relatively early age; or they may remain separate, as in some insectivores. Occasionally, I believe, the entotympanic portion of the audital bulla remains cartilaginous (as in some insectivores) but it is my understanding that in mammals the ectotympanic ring, supporting the membrane, is always present as an element and is always ossified in the adult. But the ectotympanic does not always occupy its primitive ectal position, as mentioned by van Kampen (1905) and others. In the adult *Dipodomys*, for instance, as in many other rodents, it is found that the annulus has migrated to a position within the entotympanic capsule, or audital bulla as we see it. The original stimulus for this is, of course, unknown, but it may be pointed out that in many rodents the tympanic membrane is disproportionately large as compared to the auditory meatus and that unless the mem-

brane developed entally within an enlarged bulla the tympanic annulus would otherwise make for a disproportionately capacious auditory meatus.

By careful dissection of the bulla of an adult *Dipodomys* it was seen that the tympanic annulus is represented by an extremely tenuous ring of bone bounding the membrane, and that this is so firmly fused to the entotympanic capsule that it is distinguishable only as a slight arcuate ridge. The direction of this, and hence of the inclosed tympanic membrane, is situated with the ventral part of the arc at a point about three-fifths the distance from the stylomastoid foramen to the anterior cornu of the bulla. The direction therefrom is approximately 45 degrees to the horizontal, and it extends to a point near the dorsal border of the lumen of the auditory meatus. The relatively immense size of the membrane will be realized when it is mentioned that in diameter it measures in excess of 6 mm. (in *D. spectabilis*), which is therefore more than three-fifths as large as is this detail in man.

Unfortunately the fetal material for determining the development of the ecto- in relationship to the entotympanic parts of the bulla has been unobtainable. I was able to secure from the National Museum, however, a juvenile but a few days old, and after the cranium of this specimen was clarified it was seen that the ectotympanic ring occupies relatively and approximately the same position as in the adult; that the formation of the posterior portion of the entotympanic has a tendency to precede the extension of the anterior cornu; and that at this age the medial part of the entotympanic is ossified while the lateral part, near the meatus, is as yet without sign of ossification.

Thus in *Dipodomys*, and apparently in other heteromyids and geomyids, the ectotympanic is not ectal in situation, but is covered by entotympanic features, and thus all the superficial details of the audital bulla proper are composed of entotympanic elements.

As previously mentioned the external auditory meatus is somewhat projecting in the less specialized heteromyids but this is not the case in *Dipodomys*, in which the orifice is flush with the surface contour. In all of these the lumen is more or less cylindrical, in *Dipodomys* with a very slight recess dorsally. In the jerboas, however, there is a very definite vestibule or recess, located dorsally and just within the orifice, into which opens the fenestration from the mastoid sinus. As mentioned, in life this is covered by a delicate, transparent membrane. In the kangaroo rat, therefore, the great mastoid sinuses, undoubtedly developed as a resonating apparatus, communicate solely with the middle ear. In the jerboas this apparatus can act as

a sounding board by means of a membrane of its own, situated in the outer ear, and independent of the tympanic membrane.

The contour of the audital part of the bulla has already been described. In the animals under consideration the composition of the capsule is of two sorts. In *Thomomys* and the pocket mice (both *Perognathus* and *Chaetodipus*) this is quite thick and finely cancellous, so that the cavernous part of the audital bulla, and hence of the tympanic membrane, is smaller than surface details would indicate. In all the others there is no cancellous tissue, the bony walls being thin, hard and either single, or double (*Liomys*), the inner wall being incomplete and separated from the outer wall by a very shallow space, the two being joined by numerous bony struts. Because of this difference in the thickness of the bulla wall the tympanic cavity of *Liomys* is actually larger than of some pocket mice (*Perognathus*) with larger bullae.

Removal of the inferior part of the audital capsule, and of the tympanic membrane, of these rodents with enlarged tympanic features reveals the details of the middle ear with remarkable clarity. It is seen that in reality the malleus and incus are suspended along the lateral border of the superior mastoid fenestration (between superior mastoid sinus and cavum tympani proper) at only two points. Laterorostrally the point of attachment is the anterior ligament of the malleus, from the anterior process of this bone to a process upon the margin of the fenestration; and mediocaudally by the posterior ligament of the incus, from the short process of the incus into the fossa incudis. This line of suspension of the malleus and incus appears to be correctly placed for giving great delicacy of vibration at the articulation between incus and stapes.

The manubrium of the malleus is long, slightly spatulate, and flattened along the entire border that is attached to the tympanic membrane. It ends laterally in a short processus lateralis. There is a strongly characterized manubrial lamina, absent in many rodents, directed at a right angle to the membrane, and the superior margin is slightly expanded, so that the lamina is slightly bimarinate. At about the middle of the superior border of the lamina is a small process for attachment of the extremely tenuous m. tensor tympani. From the ventral aspect it is seen that a long, sharp, processus anterior is directed cranio-laterally from the base of the manubrium, for attachment of the anterior ligament. This process, parallel to the axis of the head of the malleus, is attached, throughout the greater part of its length, to the latter by an extremely delicate lamina. The

head of the malleus is rounded and there is no well defined neck or peduncle. The articular surface is broad. In *Microdipodops* the malleus is essentially similar, nor greatly different in the pocket mice, save that the muscular process is at the base of the manubrium. In *Thomomys* the plan is much like *Dipodomys* but with different proportions.

In the jerboas the chief difference in the malleus is in the fact that the part of the head anterior to the manubrium is not rounded, with a distinct, elevated, anterior process. On the contrary it appears as though a long anterior process had supplanted the rounded anterior part of the head of *Dipodomys*. The processus muscularis was at the manubrial base, but no process for the attachment of the opposite end was distinguishable in *Scirtopoda*, although in *Dipus* the process was better defined, with much more capacious foramen for the accommodation of the m. tensor tympani, than in *Dipodomys*. In both of these genera there was an anterior ligament of the malleus and a posterior one of the incus much as in *Dipodomys*, but in addition there was accessory suspension of the ossicular chain by a wisp of tendon extending cranially and another caudally, from the processus lateralis of the manubrium. These were attached to the processes at the ventral terminations of the arc of the mastoid-ectotympanic fenestration. In other words the thin, transparent membrane which occupied this fenestration had a ventral border, between the horns of the surrounding bony arc, that was largely tendinous, and in the middle of this tendon was attached the processus lateralis of the manubrium. The important point in this connection is not that there is accessory suspension of the ossicles in these two jerboas, but rather that in one group of highly specialized saltatorial rodents there has been developed, apparently as an aid to hearing, an accessory membrane of the cavernous part of the mastoid, and that the ossicular chain has taken advantage of this circumstance in a manner that is highly suggestive of the thesis that the accessory membrane aids in transmitting sound through the ossicles to the inner ear.

It seems that the details of the malleus are largely correlated with those of the incus. Both are very different from the condition in the wood rat, for instance, in which the suspension is triangular (three-point) rather than essentially linear (two-point), while the articular process of the incus is more at a right angle with the manubrium, rather than largely parallel, as in *Dipodomys*. This is essentially the same scheme as obtains in the jerboas, and although it may well be that this ossicular arrangement is more efficient in the transmission

of certain sounds, than is that of the wood rat, still this can not be considered as a saltatorial modification, for it is encountered in the pocket gopher, among other rodents.

Cockerell, Miller and Printz (1914) have characterized the incus of the kangaroo rat as a very remarkable bone, but I am unable to detect any very significant dissimilarity from this bone in other rodents having the same general type of ossicular suspension. In *Dipodomys* the articular surface, and hence the head, of the incus is of generous size, and the crus breve, attached to the fossa incudis by the ligamentum incudis posterius, is essentially on a straight line with the malleus-incudial axis. The articular process, or crus longum, diverges somewhat from the parallel position with respect to the manubrium of the malleus, but its situation when considered together with the stapes may be judged as parallel, or rather as at a fair right angle with the ossicular axis. There is a disk-like lenticular process attached to the crus longum by an extremely fragile and constricted peduncle, prone to breakage during dissection. This articulates, by a synovial joint, with the equally disk-like capitulum of the stapes.

Broadly speaking this type of incus is encountered in all the mammals mentioned (including squirrel, pocket gopher, and jerboas) except the wood rat, although there is variation in the proportions, especially of the articular process. In the two groups of *Perognathus* (but not *Liomys*) the peduncle of the latter process is excessively flattened, or ribbon-like, and this, in slightly different form, is also a character of the jerboas examined.

The stapes of *Dipodomys* is rather broad and short, of such size that the intercrural fenestra is practically filled by the stapedia canal, and with disk-like capitulum. The processus m. stapedius is very poorly defined, and the basis stapedis bullate to a degree where the form is almost hemispherical. The latter character obtains to various degrees in all heteromyids and geomyids, apparently. In *Microdipodops* the crura of the stapes are quite remarkably elongated—a characteristic which makes the whole bone unusually long with respect to the other ossicles.

The stapedia canal has already been described. In *Dipodomys* this is a completely bony canal for the passage of the stapedia artery, which enters the tympanic part of the bulla near the basioccipital, borders the fenestra rotunda and the base of the cochlea, passes between the crura of the stapes and emerges into the endocranium. It is probable that a stapedia artery exists in every mammal at some stage of its development. This is a development of the second

aortic arch and in man persists until the middle of the third month of fetal life. In many other mammals it also disappears at some ontogenic stage, while in still others it persists without calcification, and again, as in *Dipodomys*, passes through a completely bony tunnel, which apparently is integral (fused) with the cochlear and entotympanic elements, as is the case in all the Heteromyidae. A complete stapedia canal is present in the squirrel, and in *Microdipodops* also, although in *Perognathus amplus*, representing the silky pocket mice, there is evidence that in spots the calcification has become arrested before completion. In *Perognathus baileyi*, as representing the hispid pocket mice, the bony canal is capacious and complete practically to the stapes, where it ends abruptly and the unprotected (save by soft tissue) artery thence passes between the stapedia crura. It is then a simple step to the condition as found, for instance, in the wood rat, where the canal has disappeared, leaving merely a well marked sulcus to indicate the path of the large artery, which enters the bulla near the paroccipital process. Still another situation is encountered within this and related groups, however. In *Liomys* the artery has apparently disappeared but the bony "canal," without a lumen, persists as far as the stapes and the position of the original foramen adjoining the basioccipital is indicated by a small fossa. In *Thomomys* this process is carried even farther for the solid "canal" passes uninterruptedly through the stapes.

In the jerboas there is a large stapedia artery and at least a part of the canal appears always to be present. An interesting condition is encountered in this group. The dorsal part of the canal (corresponding to the arterial sulcus in the wood rat) is formed by the petrosal, in these rodents distinct from and unfused with the entotympanic. The more ventral portion, or "roof" of the canal, however, is formed of the entotympanic element and this part may be incomplete, enclosing from a third to practically all of the artery as far as the stapes.

In *Allactaga* the petrosal and entotympanic elements are very sharply differentiated indeed. The view within the entotympanic from the ventral aspect discloses the cochlea, including the margins of both the fenestra and a portion of the sulcus of the stapedia artery, as forming the petrosal element that has intruded within the surrounding entotympanic capsule and remained unfused. This is so to only a slightly lesser degree in *Sciurtopoda* and *Dipus*. In *Allactaga* there is a definite tendency for the entotympanic to send a thin lamina of bone to cover the medial part of the stapedia artery and a small

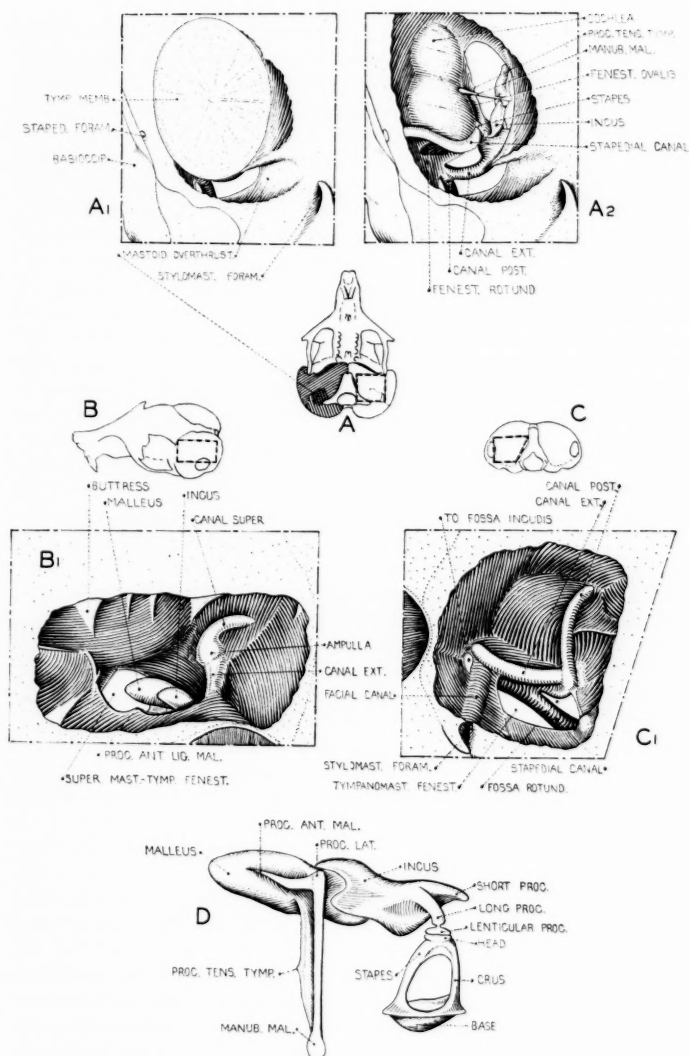


FIGURE 26. Details of the middle and inner ear of *Dipodomys*, showing sketch outline of skulls (A, B, C) indicating areas inclosed in broken line which, in the other items, are shown greatly enlarged and with their bony walls broken away. (A2) is a deeper view of (A1).

portion of the adjacent bone. This is more pronounced in *Scirtopoda*, while in *Dipus* fully half of the ventral part of the cochlea is so covered. The result is that in the jerboas the dorsal wall of the stapedial canal is petrous, and the ventral wall, or that part of it which occurs, is always entotympanic.

In gross features the semicircular canals of *Dipodomys* are hardly worthy of note, save in respect to their quite remarkable freedom from the usual amount of surrounding bony tissue, especially within the posterior mastoid sinus. They are quite similar in conformation to those of other mammals, the superior and posterior canals being in the vertical and the lateral in the horizontal plane, or virtually so. The plane of the superior canal is at an angle to the sagittal plane of about 45 degrees, as is probably invariably the case in the Mammalia.

There are many details of the physiology of hearing about which we know little or nothing. It seems quite likely, however, that in respect to the labyrinth a short cochlea with few coils of the sort found in at least some of the Insectivora represents a considerably more primitive, or less specialized, mammalian condition than does one with more coils. As some of the rodents are equipped with a greater number of coils than representatives of any other mammalian order, so far as known, it appears justifiable to assume that the auditory equipment of such rodents is in *some* respects more efficient than of any other mammals. But whether this takes the form of increased keenness of exactly the human type of hearing cannot be told. In *Dipodomys* there are not an unusual number of cochlear turns but at least it is likely that its great sinuses have introduced into the situation an acoustic element about which we can only speculate.

The cochlea of *Dipodomys*, in ventral aspect, is not merely a slight swelling of the bony surface as is the case in the wood rat, for instance, but is sharply marked off from the surrounding bony features as in the squirrel, and is rather thin-walled. In all the heteromyids and geomyids examined the capsule of the cochlea is apparently fully fused with the bordering entotympanic element. In the squirrel and wood rat (and many other rodents) a sutural line is definable, and in the jerboas this is very distinct, to the extent in *Allactaga* at least where it is probable that the cochlea is attached to the bordering entotympanic only by connective tissue.

At the base of the cochlea caudal to the stapedial canal or artery there is the fenestra rotunda, opening into the scala tympani, and giving access to the scala vestibuli is the fenestra ovalis, into which fits the basis stapedis. In the wood rat, squirrel, and *Dipodomys*

there are from two to two and a half spirals of the cochlea. But in other respects the cochlear features of the kangaroo rat are different. In the first place the cochlear capsule in the wood rat and squirrel is short, relatively broad, and subglobular in form. In *Dipodomys* and *Microdipodops*, but not to any marked extent in *Liomys*, *Perognathus* or *Thomomys*, the cochlear capsule is much elongated and has a definite central constriction. It will be found that in all these rodents the part of the scala represented by the lower three-quarters of the first turn is much larger and more capacious than the part more apically situated, and it is this larger, basal portion that is contained, in the kangaroo rats and mice, within the basal expansion of the cochlear capsule, while the remainder is contained within the part above the constriction.

In *Dipodomys* the lamina spiralis ossea was much reduced in breadth as compared with the squirrel and pocket gopher, with the canalis spiralis relatively more capacious. The elongation of the capsule in these two genera was accompanied by spirals that were considerably steeper, and hence much longer in comparison with the width.

In the jerboas there were also slightly more than two spiral turns to the cochlea, which was subglobular and entirely comparable to the condition in the wood rat and squirrel, rather than in the kangaroo rats and mice.

Occipital. The occipital is, of course, composed of supra-, ex-, and basioccipital elements and in *Dipodomys* this complex is hardly less remarkable than that of the temporal.

In the squirrel the occipital is of generous proportions. The mastoid indents the border of the complex between the ex- and supraoccipital elements, and there is a prominent paroccipital process of the exoccipital. In the wood rat the exoccipital is narrower and the supraoccipital sends a long, narrow process ventrally in front of the mastoid, this forming the extreme distal part of the well defined lambdoidal crest. In *Thomomys* this supraoccipital process is represented as much broader, and the crest is correspondingly broad and less sharp. The paroccipital process is also absent as such, but it is represented by a ridge, and the exoccipital covers the entire medial part of the mastoid in a thin lamina. This may very well represent the condition occurring in the ancestral form of the Heteromyidae. In *Liomys* the lambdoidal process of the supraoccipital has become smaller, the exoccipital lamina covering the mastoid has shrunk and retreated medially, and the paroccipital ridge has assumed the form of a blunt and rather broad process. These steps are carried

farther in the hispid pocket mouse (*P. baileyi*) and in addition the increasing size of the mastoid has restricted the parietal to the region entirely rostral to the interparietal. Accompanying this situation the exoccipital has sent a slender process rostrally along the lateral border of the interparietal. In the silky pocket mouse (*P. amplus*) the width of the supra- and exoccipitals is still more reduced, save for the paroccipital process, which extends more lateral than ventral. The anterior process of the supraoccipital, bordering the interparietal, is still present and extremely slender. The culmination of these various steps is encountered in *Dipodomys deserti* and *Microdipodops* (in ratio to bulla development) in which all the occipital elements save the paroccipital process are as much reduced as they could well be, the part of the supraoccipital visible from the dorsal aspect being merely a thin sliver of bone, and the remainder as narrow as the articulation with the atlas will permit.

An analysis of the situation accompanying the reduction of the heteromyid occipital, as followed above, discloses an interesting situation. In the Mammalia the musculature inserting upon the occiput is always confined to this plane. In other words it apparently is incapable of shifting its attachment to the parietals or interparietal, but if there be a need for an altered angle of leverage of the muscles involved this is accomplished by a tilting of the entire occipital plane. But it is entirely feasible for the muscles inserting along the lambdoidal crest to shift from mastoid process of the mastoid to the mastoid process of the squamosal, or from the latter to the supraoccipital border. In *Microdipodops* and *Dipodomys deserti*, however, all of these muscles may be considered as confined to the mastoid alone, for the superior part of the supraoccipital is too insignificant to furnish an appreciable area for attachment.

In the jerboas a somewhat different principle is involved. In *Scirtopoda* and *Dipus* at least, and probably in some others, it is clear that the occipital has not been gradually crowded medially as the bulla enlarged, but rather that the latter has first developed *beneath* the occipital, and that later the overlying occipital lamina has disappeared except along a line corresponding to the position of a lambdoid ridge, which persists as a thin laminar process extending ventrally behind the auditory meatus. This process has disappeared as well in forms with yet larger bullae (*Salpingotus*).

It seems to be beyond question that small saltatorial rodents of the sorts under consideration are in the habit of carrying the body more erect, and hence the head tilted forward at an angle with the

body axis, to a considerably greater degree than is the case with the wood rat, for instance. It would therefore be expected, in accordance with the arguments that I have already advanced (1930) in discussing aquatic mammals, that they would have the occipital plane tilted farther to the rear, but comparison with generalized rodents of a variety of sorts shows that this is not the case to any very marked degree. I suspect that this is attributable to a variety of causes, among which is small size, for in the much larger *Pedetes* the backward tilt of the occipital plane is very marked. Then two the smaller heteromyids and jerboas have small, light occipital condyles that are located farther ventral than normal, and it is felt that neither this feature nor that of the unusually rounded conformation of the lambdoidal area can be properly evaluated at this time.

It may be mentioned that *Allactaga* is the only saltatorial rodent examined whose maxillary incisors project to a marked degree. This is popularly presumed to be a development enabling the animal to employ the incisors as a pick for loosening the ground while constructing burrows.

Mandibles.

The mandibles of rodents that are saltatorially modified to the degree that the bullae are of phenomenal size are notable for their weak coronoid processes, following reduction in size of the temporal

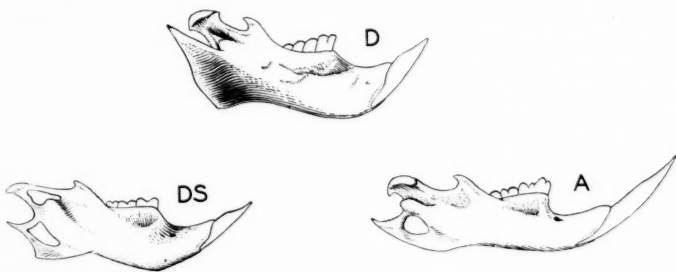


FIGURE 27. Right mandibles (\times about $1\frac{1}{2}$) of *Dipodomys* (D), *Dipus sowerbyi* (DS), and *Allactaga* (A).

muscles, and for lateral extension of their angular processes. The latter condition is correlated with the fact that in *Dipodomys* especially, and to a lesser degree in *Microdipodops* and probably *Salpingotus*, the glenoid fossa does not immediately adjoin the zygomatic root of

the squamosal but is somewhat medial to it. Hence, efficiency dictates that in the mandible the insertion of the masseter, upon the angular process, should be somewhat lateral to the condyle. In *Allactaga* the mandible is slender and weak, with low condylar process, the fragility of the posterior part being carried to the point where there is a large fenestration in the bone at the base of the coronoid process. This is also the case in the *Scirtopoda* dissected, while in *Dipus sowerbyi* there is an additional fenestration at the base of the exceedingly weak condylar process (fig. 27). The latter condition is shown to obtain also in *Scirtopoda lichtensteini* at least, according to Vinogradov (1927), but no mandibular fenestrations are shown in the same author's (1922) drawings of *Salpingotus*.

Trunk.

It is extremely likely that if the different segments of the vertebral series could be properly evaluated with each other and with actual body size the results would be very significant in such a study as the present one. The difficulties encountered are very great, however. For example, if the cervical series be compared with trunk length and is found to be relatively shorter in one animal than another, it is impossible to tell whether the result indicates a shorter neck or a longer body, for the reason that there is no standard by which the trunk length can be reduced to an identical value. This difficulty appears so serious that it is considered inadvisable to attach much importance to such comparisons unless they are corroborated by other details, or very seriously to evaluate extensive series of vertebral measurements of all available saltators, on the grounds that they would probably be misleading.

Cervical vertebrae. A mobile head at the end of a neck of considerable length may be employed very effectively as a balance. In aquatic, cursorial, and saltatorial mammals of a high degree of specialization the tendency is for the development of a single, highly efficient equilibrator and the suppression of accessory balancers. Hence, as the tail of *Dipodomys* is so well developed for this purpose one might expect to find the neck somewhat shorter than in the wood rat for instance. That such is not as yet the case to any marked extent may be attributable in part to the fact that the neck in rodents of usual rat-like form is already somewhat shortened. Additional shortening has occurred, however, to a definite degree in the more highly modified *Scirtopoda* (cervical series 8 per cent of the body length; 12 per cent in *Allactaga*, *Pedetes*, *Dipodomys*; and 12.5 per

cent in *Neotoma*). But perhaps this is not altogether the proper way for comparison, for the atlas and axis have certain rotary functions to perform which leave these two details less affected (at least up to the point where fusion of the vertebrae occurs) by a shortening stimulus than the other five cervical elements. It may be more proper and significant to state that in a *Neotoma* skeleton the five posterior cervicals are almost as long as four ($3\frac{4}{5}$) of the anterior thoracics; in *Pedetes* and *Allactaga* the comparable figure is $3\frac{1}{3}$; in *Dipodomys* about 3; and in *Scirtopoda* less than 3.*

In a generalized, quadrupedal rodent there is a very real need for definite mobility of the head and neck while seeking food and during other activities. In a rodent of marked saltatorial adaptation, in which the hind limbs have increased out of proportion to the fore limbs, mobility of the head is in some respects relatively needless and in others disadvantageous. It is of disadvantage to the extent that the effectiveness of the tail as an equilibrator is lessened by a mobile neck: and it is needless because when the animal wishes to indulge in elevation or depression of the head this will be accomplished less by individual movement of this element, as in a generalized form, than by the tendency to accomplish this end by a tilting of the entire body, through the hip joints as a pivot. By this procedure there is little or no necessity for independent movement of the head in the sagittal plane.

Aside from slight difference in the form of the well defined spinous process of the axis, some little variation in the transverse processes of the atlas, and in the degree of fusion of the elements, the cervical series of the genera under consideration do not differ from that of the generalized rodent. In both the latter and the saltatorial forms the last five cervicals lack spinous processes save in *Pedetes*, in which these are slightly developed. The spine of the axis is well developed in all, but least so in *Allactaga*. All have ventral lamellar processes of the sixth cervical, chiefly concerned with the longus colli muscle; but in *Scirtopoda* these processes are weak and ill defined. Lateral prominences consist of a dorsal series, or parapophyses, and a ventral series of longer "transverse" processes, or diapophyses.

Lyon (1901) found that "in *Dipus* atlas and axis, free dorsally and laterally only, below they are fused into one piece." In all of the specimens examined by me, however, the atlas has been free of the

*This detail could be determined only approximately for these two genera because of the fused cervicals.

axis. In two specimens of *Scirtopoda* at hand the five central cervicals are completely fused, with the axial spine developed so as to surmount the entire complex, but Flower (1874) and Lull (1904) have stated that the last six are fused. It was found that in *Dipodomys spectabilis* the second and third, or second to fourth, were fused, but in some individuals of other species (as *D. merriami*) the fifth was also involved. It thus seems clear that the degree of fusion of the cervicals within this genus is individually variable though with specific trends one way or the other. That some fusion should occur in *Dipodomys* and that this character should be more marked in *Scirtopoda* is entirely expectable, this corresponding with the degree of saltatorial adaptation in other respects. But it is not according to expectation to find that *Allactaga*, which appears to be much more adept at saltation than *Dipodomys*, has all of this series free, as has *Pedetes*.

Thoracic vertebrae. The fact that in *Neotoma* and many, if not most, other rodents of a generalized nature there are thirteen thoracic vertebrae, while in all the saltatorial rodents (as well as in *Lepus*) examined there were 12, probably indicates that in leaping rodents the tendency is for a shortening of the thorax, but not of the individual vertebrae involved. The proportion of thoracic to body length accordingly varies in the smaller saltatorial sorts from 30 (*Allactaga*) and 32 (*Dipodomys* and *Scirtopoda*), to more than 35 (*Pedetes*, as in *Neotoma*) per cent of the body length. Actually, however, if one take only the first twelve thoracics in the wood rat it is found that in all these smaller rodents this series averages very much the same, and certainly the differences are too slight to be of much significance.

In *Neotoma* the first thoracic is devoid of a spine, while that of the second is long. Succeeding ones are progressively slightly smaller, and all slope rearward as far as the tenth, which is vertical. In *Dipodomys* the second is not the longest of the series and all are exceedingly short as far as the ninth thoracic. The latter is somewhat longer, and the remaining thoracics are abruptly much longer. In this animal the eleventh is the vertical vertebra. In the jerboas this plan is different to the extent that the posterior thoracics are not abruptly longer. In fact all the thoracics are very low and poorly defined, the anterior being practically absent and only those in the extreme posterior part of the series have really appreciable definition. In these it is the twelfth spine that is vertical. In *Pedetes*, however, the vertical spine is the eleventh, as in *Dipodomys*; but in this animal

the spines are all well defined and more uniform than in any of the small saltators examined.

It is thus indicated that in these saltatorial rodents there is a definite tendency for the vertical or anticlinal spine to shift caudally, in ratio to the degree of saltation, from the tenth thoracic in the generalized rodent (*Neotoma*, *Sciurus*, etc.) to the eleventh in sorts better modified for leaping (*Dipodomys*), and finally to the twelfth (jerboas), indicating a corresponding shift in the center of motion of the vertebral column and back musculature.

In the rodents under consideration the lateral muscular processes of the thoracic vertebrae, comprising met-, an-, and diapophyses, are essentially as in the wood rat, the conformation differing only in minor detail. Whereas in *Neotoma*, however, the differentiation of the transverse processes of the anterior thoracics into separate met- and anapophyses may be said to occur upon the eleventh vertebra, this takes place upon the ninth or tenth in the saltatorial forms. Hence this feature does not vary according to the position of the anticlinal vertebra.

Lumbar vertebrae. Complementary to the fact that in all rodents herein considered there are 19 thoracolumbar vertebrae, there are 7 lumbar in all the leaping sorts and 6 in the wood rat. The fact that in the jerboas and *Pedetes* the proportion of the lumbar series to body length is about 40 per cent and about 34 in *Dipodomys*, while in *Neotoma* this figure is 33 (37 per cent allowing for 7 instead of 6 vertebrae), seems to indicate that no safe correlation with saltatorial habits can be accepted for this item, save, of course, that with any diminution in the number of thoracic vertebrae there will be a compensational lengthening of the distance between thorax and pelvis.

From *Neotoma*, and to a considerable extent from *Sciurus*, the lumbar region of *Dipodomys* and *Pedetes* differs in having the spines higher (especially posteriorly) and narrower in a sagittal direction, the metapophyses higher anteriorly and lower posteriorly, anapophyses relatively better defined (but disappearing from last two or three), and the posterior diapophyses considerably better developed. On the whole these same trends are encountered in the jerboas in all details mentioned save in the anapophyses, which are smaller.

Sacral vertebrae. There are usually 4 or 5 sacral vertebrae in *Dipodomys*, 3 in *Pedetes*, *Sciurus* and *Thomomys*, and 4 in *Neotoma* and the jerboas. The sacral length accordingly varies from 13 per cent of the body length in *Pedetes* to 25 per cent in *Dipodomys*, so it is unlikely that the number of vertebrae fused into the sacral complex

has any direct relationship to saltatorial habits. Width of sacrum appears to be relatively greater in the jerboas than in the wood rat, and greater still in *Dipodomys*. It is believed that this feature, indicating breadth of a part of the back musculature, is probably a saltatorial modification in the kangaroo rat's special equipment for saltation, while approximately the same end may be accomplished in a different manner in the case of the jerboas.

The above reasoning probably applies, in different degree, to the case of the sacral spines. In *Neotoma* the sacral spines are essentially the same as the lumbar ones. In *Pedetes* the three spines of this series are firmly fused together. In *Dipodomys* the first 2, and in the jerboas the first 3, sacrals are devoid of spines. It is believed that the partial absence of sacral spines is merely the reflection of the presence of a spinalis element to the back musculature, stretching between the last lumbar and the last sacrals or first caudal, and while this may be partially attributable to saltatorial habits in these particular animals, the presence of a spinalis in this region can hardly be included in a list of saltatorial modifications.

Caudal vertebrae. The caudal length is amenable to the stimuli derived from various modes of locomotion to a greater extent than any other series of the vertebral column. Strictly cursorial mammals, or those which are even partially saltatorial, often have a tail of insufficient massiveness to constitute an effective equilibrator or counterpoise, this function being assumed by the head and neck; or the tail may be virtually absent (*Lepus*). In strictly saltatorial sorts, however, the tail must be of sufficient length and mass to function as an efficient and almost instantaneous counterpoise, while the head and neck will virtually cease to function in any such capacity. Theoretically it is possible that a saltatory mammal with no tail to speak of and a long, sinuous neck might leap about with the agility of a jerboa, but no mammal has assumed this form, unless one except the giraffe, which is too cumbersome to be saltatorial.

In *Neotoma* there are about 28 to 30 caudal vertebrae, about 30 or 31 in *Dipodomys*, 26 or 27 in *Pedetes*, and 26 to 30 in the jerboas. It is thus seen that there has been no definite increase in number of vertebrae, and comparison shows that increase in tail length has been secured by elongation of the individual vertebrae. Thus in a typical skeleton of *Neotoma* the tail is 145 per cent of the body length, about 160 per cent in the much heavier *Pedetes*, 234 in *Dipodomys spectabilis*, 241 in *Allactaga*, and 272 per cent in *Scirtopoda*. This is entirely according to expectation, at least in respect to the lighter rodents,

whose long leaps have some features in common with the flight of an arrow.

Many of the chevron bones had been lost during cleaning and no study was made of this feature. It was found, however, that they do not cease between the ninth and tenth caudals, as said by Parsons (1898) to be the case in *Dipus*, but extend quite to the end of the tail in the jerboas as well as *Dipodomys*. They become better defined in the saltators, through *Dipodomys* and then the jerboas, as representing the lighter forms. There is, however, no tendency in these mammals for the chevrons to become long and to simulate the form of a spinous process. But in the heavier *Pedetes*, as in the kangaroo, this tendency is very pronounced and in the former the chevrons near the tail base are as long and as well defined as the spinous processes of the anterior thoracics.

As saltatorial modifications increase there is needed an augmented ability to move the tail more strongly in a variety of directions, as a counterbalance, and the stronger muscular equipment needed in this connection is reflected in these saltatorial rodents by longer processes upon the anterior part of the caudal series. This is especially marked in *Pedetes*, possibly in compensation for its relatively shorter tail.

Sternum. The manubrium is individually somewhat variable in form but does not depart in essential details from that characteristic of most rodents. The number of sternebrae is also variable individually. Since reporting on the wood rat (1926) I have examined skeletons of this genus having both 3 and 5 of these elements, and there is probably equal variation in the saltators. Such differences usually mean merely that there have been fusion of two centers, in the case of a reduced number, or separation of an additional center, where augmented. The xiphoid bone was rather short in all instances except the wood rat.

Costae. As already mentioned, there were 13 pairs of ribs in the wood rat and 12 in the saltators. In *Pedetes* the first 11 ribs had both capitular and tubercular attachment to the vertebrae, the first 10 in *Neotoma* and *Sciurus*, 9 in *Dipodomys* and 8 in the jerboas. Reduction in the number of ribs with tubercular attachment is supposed to allow an increase in the mobility of the chest wall, but it is difficult to understand how this feature would be of benefit to saltation.

Extremities.

Clavicle. This bone was present in all individuals but it had no unusual characters.

Scapula. There is but slight relative difference in scapular length among those species considered, but there is considerable variation in other details of this bone. Whereas *Neotoma* has the supraspinous fossa about equal in width to the infraspinous, in the saltators the former is much the narrower, especially in *Dipodomys*, *Pedetes*, and *Sciropoda*, a character which accompanies reduced width of the supraspinatus muscle. The latter fact seems not particularly significant, for the function of this muscle is intimately connected with that of the infraspinatus. The narrower scapula of these saltators is accompanied by a falciform Glenovertebral angle, and this in turn is accompanied by a pronounced broadening of the teres major attachment over its lateral surface. And by the falciform projection of the bone the serratus magnus is given better leverage for depression of the posterior part of the scapula, and hence anterior elevation of the arm, than would otherwise be the case. Increase in the effectiveness of the teres major might very easily be translated into a better ability in digging than the size of the anterior limb might indicate.

The acromion is narrower in the saltators and the coracoid relatively shorter, especially in *Dipodomys*, than is the case in either *Neotoma* or *Sciurus*. The latter feature apparently reflects a corresponding weakness in the development of the short head of the biceps, but as the latter was present in the kangaroo rat and absent in the jerboas it is surprising that the coracoid was weakest in the former.

In most mammals the anterior limb is shorter than the posterior, and plays a lesser rôle in locomotion. Even in the strictly cursorial sorts the hind limbs usually furnish considerably more than 50 per cent of the propulsive force, while the anterior members are more exclusively concerned with support. It must also be borne in mind that even those rodents which we are accustomed to consider as fairly generalized in major features are to a slight extent saltatorial; this has had an undetermined effect upon limb length.

When the arm length, considered in this instance as comprising the combined measurements of humerus and radius, are compared with body length it is found that any reduction in relative arm length that may have occurred cannot be appreciated in this manner, for the percentages are 46 for *Dipodomys*, 45 for *Neotoma*, 42 for *Sciropoda*, 41 for *Allactaga*, and 40 for *Pedetes*. What has actually occurred is probably some slight shortening of the arm in the saltators, which gives the appearance of being enhanced both by a shortening of the body and by a lengthening of the hind limb. Certainly, however,

the arm has not lost as much as the leg has gained in functional length.

Humerus. In comparison with the radius the brachial segment is of the same or greater length in *Neotoma* and *Pedetes*, and definitely shorter (44 to 46 per cent) in the other saltators. As this detail varies largely according to group in other mammals there is no reason for assuming it to have adaptational significance in the present case.

In *Dipodomys* the humerus shows practically no bicipital groove. In comparison with *Neotoma* the deltoid insertion is more spinous, with less of the form of a crest or ridge, reflecting the more circumscribed origin of the deltoid muscle in *Dipodomys* (and the jerboas). The anterior part of the greater tuberosity is very poorly defined, for some obscure reason, but the lateral part is much as in the wood rat. The lesser tuberosity is slightly higher. The lateral epicondylar ridge is relatively broader and the trochlea is located a bit more medial in respect to the humeral axis. There is an entepicondylar foramen in *Dipodomys*, as in the wood rat, and in the former only among the animals dissected is there a well formed sesamoid bone within the original tendon of the supinator and located directly lateral to the radial head.

The jerboas agree in having a bicipital groove, with the anterior part of the greater tuberosity well defined but lower than in the wood rat, while the entepicondylar ridge is not quite so broad but extends farther proximally. There is no entepicondylar foramen. In a specimen of *Pedetes* the latter is present, although it did not occur in an adult which Parsons (1898) dissected. In this animal the insertion of the deltoid was indicated not by a sharp process, but by a broad, blunt rugosity.

Radius and ulna. Length of forearm has already been given. Otherwise there are few details of any significance. In *Neotoma*, *Dipodomys* and the jerboas these bones are all very similar, and all show the same tendency to develop a thin lamella of bone upon the radial border of the ulna to supplant in large degree the interosseous membrane. This is not the case in *Pedetes*, however. In *Dipodomys* the "falcate process" of the ulna is knob-like with a slightly constricted neck, so that at a casual glance it is easily mistaken for a carpal bone. Adjoining it, but upon the volar aspect, is a knob-like process of the radius. Neither character is present in the jerboas.

Manus. The manus of *Dipodomys* is entirely comparable to that of *Neotoma*, differing from the latter only in details that are relatively

minor. It consists of a broad scapholunar, ulnare (triquetrum), a large pisiform extending well to the volar surface of the lateral border of the hand; a large, long, and strong medial sesamoid which completely bridges the long flexor tendons of the hand and which articulates with the pisiform; a centrale, first (multangulum majus), second (multangulum minus), and third (capitatum) carpale, and an unciform (hamatum). In *Allactaga* the second carpale was more medial than strictly proximal to the second metacarpal. In this animal there was a small sesamoid on the dorsum of the manus, located between the radius and the medial part of the scapholunar. It was not possible to determine this point in the more completely cleaned skeleton of *Scirtopoda*. The latter, however, exhibited the character of the second carpale described for *Allactaga*, but the scapholunar was narrower (transversely), more spherical, and less strap-shaped, while the ulnare was correspondingly broader.

No study of the disarticulated bones of the manus was undertaken, and the only features apparent in the articulated skeletons as worthy of note were the facts that in *Allactaga* the claws were shorter and the digits correspondingly longer, especially the second phalanges, than in *Scirtopoda*. In addition there was, in *Dipodomys* and the jerboas, a definite process, proximally directed, upon the dorsum of the pollex at the base of the nail. In *Dipodomys* this has the appearance of being a sesamoid bone between the first and second phalanx, while in *Scirtopoda* it is better developed and seems to be completely fused with the terminal phalanx. Neither manus was articulated in the skeleton of *Pedetes*.

Pelvic girdle. The components of the innominate bone are thoroughly fused in all the specimens examined, so that the precise limits of the individual bones cannot be defined. The attachment of the innominate to the vertebral column is at the anterior part of the sacrum, and the angle of the pelvic axis with that of the column is about the same in all animals examined.

The total length of the innominate is not very significant in the present study, for length of ilium especially is dependent upon many diverse factors. The innominate is about 48 per cent of the body length in *Dipodomys*, 47 in *Scirtopoda*, 42 in *Pedetes*, 39 in *Allactaga*, and 35 in *Neotoma*, and it is not possible to make much use of such an array of figures, especially when it is considered that body length is also reflected thereby. A much more significant comparison is that of the postacetabular to the preacetabular measurement of the pelvis. The former, expressed in percentage of the latter, is

66 per cent in *Neotoma*, 62 in *Pedetes*, 71 in *Dipodomys*, 81 in *Allactaga*, and 94 in *Scirtopoda*. These figures may, of course, indicate that there has been experienced by the saltatorial forms either a shortening of the ilium, a lengthening of the ischium, or both. Comparison of specimens seems to indicate that there has been a definite alteration in both elements, but that that of the ilium is the more pronounced, and that the degree of change is in direct ratio with saltatorial specialization.

But this feature may be further analyzed. Is it the part of the ilium from acetabulum to sacral attachment, concerned chiefly with the mechanics of pelvic and hind limb support, or the portion from sacral articulation to the iliac spine, more concerned with muscular and ligamentous considerations, that is chiefly concerned? If the distance from the center of the acetabulum to the center of pelvisacral articulation be designated as the postsacral portion of the ilium, and the distance from the latter point to the tip of the iliac spine as the presacral, then the percentage of the postsacral to presacral measurement is 70 per cent for *Neotoma*, 96 for *Dipodomys*, 110 for *Allactaga*, 112 for *Pedetes*, and 117 for *Scirtopoda*. These figures are very definitely suggestive of the thesis that as saltatorial specialization of rodents increases there is alteration in the (chiefly) mechanical requirements, that will shorten the distance between the hip joint and the sacral articulation, and that this is correlated with (or apparently followed by, in this group) a further but less pronounced, shortening of the anterior ilium.

I am entirely unable to convince myself that a long ilium, projecting far forward of the hip joint, can have been developed, or retained, because of active muscular advantage alone, for there are no really important muscles attached to the anterior ilium that would not seem to function approximately as well if this bone were shorter. But the *passive* muscular, and ligamentous, advantage should be relatively great. Surely muscles and ligaments of fixation would operate to better advantage from a relatively long presacral extension of the ilium in furnishing leverage to counteract any strain put upon the pelvis by postsacral stress. This is an interesting possibility to consider but it can by no means be accepted until more is known of the contrary conditions encountered in some of the primates, as shortly to be discussed by W. L. Straus, Jr.

Other major details of the ilium comprise the vertical dimension, or width, and the degree of lateral divergence of the spines. In *Dipodomys* the distance between the ilial spines is about the same as

in *Allactaga*, but they flare more in the latter for the reason that the sacral width is less. These details are largely dependent upon the conformation of the lateral part of the longissimus dorsi, attached to the medial ilium. In *Scirtopoda* this detail was relatively poorly developed and, as might be expected, the interspinal measurement is less. Vertical measurement of the ilium is apparently correlated with requirements chiefly of the glutei minimus and quartus (scansorius) and of the iliacus, although the other muscles attached to the ilium undoubtedly have some effect in this connection. Attention should be called to the fact that in *Scirtopoda* the gemellus superior reaches practically to the spine of the ilium.

The relative size of the superior and inferior gluteal fossae is a puzzling detail. In *Ncotoma* and *Dipodomys* the superior is very noticeably the larger, while in the jerboas and *Pedetes* this is so of the inferior fossa. I am unable to correlate this with muscular attachments for the reason that the gluteus minimus may occupy one fossa in one genus and the other in another. The muscles which have their chief attachment upon the spine of the ilium are the glutei superficialis and medius, and to a lesser degree the iliacus, but the differences existing seem not to be correlated with variations in the shape of this bony detail.

The rectus femoris process of the ilium was slightly smaller in *Dipodomys* than *Ncotoma*, still more reduced in *Scirtopoda*, and absent as a process in *Allactaga* and *Pedetes*; but corresponding differences in the muscle were not detected.

There are various factors that must be considered in discussing the posterior pelvis. For instance it is almost impossible to place a proper valuation on symphyseal details. We know nothing about the requirement of strength in this structure, or the amount of spreading that takes place in the different sorts of mammals during parturition. Needless to say the latter factor is the most important consideration in the shaping of the pelvis, for the variant developing a pelvic architecture which does not allow the passage of the young is summarily eliminated, and no contrary stimulus, no matter how vigorous, can have any effect on the species.

In this connection the details of the symphysis pubis may or may not be of importance, according to genus. Presumably, as in some other rodents (guinea pig, pocket gopher), there is a softening of the connection and a lengthening of the connecting fibers to various degrees, according to group requirements, when the young are born. At any rate the symphysis is about as long in *Dipodomys* (3.7 mm.)

as in the wood rat, longer in *Allactaga* (6.4 mm.), and unusually extensive in *Scirtopoda* (11.4 mm.). In the latter genus the pelvic arch is pronouncedly and acutely V-shaped, but U-shaped in *Dipodomys*, with *Allactaga* occupying an intermediate position.

The relatively longer postacetabular measurement of the innominate in the saltators allows for a somewhat more effective leverage for the muscles attached posteriorly, with function of retracting the thigh and flexing the shank, only the former of which actions is primarily helpful during saltation. The mechanical and numerous muscular stimuli that combine to cause the variation in the minor details of the ischium and pubis are so inextricable that it seems unwise to attempt their interpretation. It may be pointed out, however, that while in *Neotoma* the superior tuberosity of the ischium is directly vertical to the inferior tuberosity, as is the case in *Scirtopoda*, in *Allactaga* the inferior tuberosity is anteriorly, and in *Dipodomys* posteriorly, situated in relation to the superior tuberosity. All four saltators, including *Pedetes*, are characterized by the lateral projection of a spinous process upon the superior tuberosity of the ischium, which, however, in *Dipodomys* assumes more the form of a crest. This is most likely attributable to the increased efficiency, and stronger, more tendinous origins, of these components of the hamstring muscles thereto attached, and which, in connection with fixing action by the extensors of the shank, are of major use in the retraction of the thigh. In *Pedetes* the ischial tuberosity is projected dorsally so as almost to be falciform. Both *Dipodomys* and *Pedetes*, but not *Neotoma* nor the jerboas, have a sharp ischial spine, marking the anterior limit of the obturator notch, upon the superior border of the ischium. This is undoubtedly correlated with the fact that in the two genera the obturator internus is double, and the notch is a necessity for the proper guidance or confinement of the tendon passing from the anterior division of this muscle.

Before considering the individual bones of the posterior extremity it will be desirable to make some comparison of the limb as a whole. In the case of mammals with non-elongated carpal and tarsal elements the usual intermembral index 1^* is significant, and for mammals of the general organization of the wood rat this would doubtless prove to be entirely satisfactory. As a matter of interest it may be given for the others. The intermembral index is accordingly 74 in *Neotoma*,

$$*1^* = \frac{\text{humerus} + \text{radius} \times 100}{\text{femur} + \text{tibia}} = \text{intermembral index.}$$

96 in *Lepus*, 46 in *Dipodomys*, 48 in a large kangaroo (*Macropus*) of undetermined species, 39 in *Pedetes*, 38 in *Scirtopoda*, and 36 in *Allactaga*. But whereas in these genera the humerus plus radius does equal functional length of arm (if one except the short distance from the radius to the palm), the femur plus tibia is not the functional length of leg, for these mammals are largely digitigrade, at least in locomotion. Theoretically the leg length should be the distance from the head of the femur to the knee, thence to ankle and finally from the ankle to point of the anterior foot from whence is applied the final leaping impulse. This is some point between the anterior end of the metatarsus and the tip of the toes, impracticable of precise determination. So for saltatorial mammals the intermembral index should be modified by adding to the sum of femur and tibia the distance from the center of the ankle joint to a point representing the average anterior termination of the three or four longest metatarsals. The index is then 60 for *Neotoma*, 35 for *Dipodomys*, 30 for *Pedetes*, and 25 for both *Allactaga* and *Scirtopoda*. This probably represents with a satisfactory degree of accuracy the respective saltatorial attainments of the genera in question.

Femur. Comparison indicates that the percentage of the femur to body length is about 31 in *Neotoma*, 42 in *Pedetes*, 43 in *Dipodomys*, 47 in *Allactaga*, and 49 in *Scirtopoda*. But it must be remembered that this also reflects relative difference in body length. A more satisfactory treatment would seem to be to express the proportion of the femur in percentage of the sum of femur, crus and pes reduced to 100. The value of the femur is then 35 in *Neotoma*, 28 in *Dipodomys*, and 24 in *Allactaga* and *Scirtopoda*, indicating relative reduction in the length of this segment accompanying elongation of the limb.

Compared with *Neotoma* the femur of *Dipodomys* has the greater trochanter higher with respect to the head, and the third trochanter as well is situated more proximally. This indicates an increase in the leverage of the gluteus medius complex and probably a tendency toward the speeding up of the action of the gluteus superficialis and adductor brevis, inserting upon the third trochanter. Similarly compared the femur of the jerboas has a relatively larger neck situated more nearly at a right angle to the shaft, which latter is more slender. The greater trochanter is also higher, and this is especially marked in *Pedetes*. In the saltators there seems to be a tendency for the trochanteric or obturator fossa to extend toward the lesser trochanter, culminating in *Pedetes* in which the fossa includes the base of the latter trochanter, thus theoretically increasing the strength of move-

ment of the femur to the rear during leaping. The absence of a third trochanter in *Pedetes* and the jerboas is a group character and has nothing to do with saltation.

There were many minor differences in the attachments of the thigh musculature, but these are difficult to evaluate precisely and it is felt that none of them were of outstanding, or at least clearly apparent, significance in regard to saltation. Some consideration, however, should be given to probable trends.

As is well known a high degree of cursorial or saltatorial specialization is conducive to the confinement in a single plane of the movements of the joints of the limbs employed in propulsion, and the reduction of possible movement in other directions. This means that, theoretically, all muscles that can aid in simple flexion and extension of the limb segments will be developed, while those which normally accomplish abductive, adductive and rotational action of the member will tend toward reduction unless they prove to be of importance for fixation during action of the flexor and extensor groups of muscles. In addition it would be expected that there would be a simplification of the musculature and a trend toward the consolidation or partial fusion of the components of the several groups—a tendency toward the fusion of the elements of the quadriceps femoris, or of the adductor mass, for instance.

It may be noted that the psoas minor was weak in all specimens dissected, while the psoas major was well developed, but to a lesser extent in *Scirtopoda*. The vastus medialis was especially extensive in *Dipodomys* and smaller in the jerboas. The tendency shown for the fusion of some of the shorter hip muscles is often encountered in rodents, but it should be noted that the obturator internus was double in both *Dipodomys* and *Pedetes*, although weak in the jerboas. It appears that there is a tendency in the saltators, most pronounced in *Allactaga*, for partial fusion of the adductor mass, and in the animal mentioned one head of the semimembranosus is also involved. In the jerboas the adductor magnus is relatively more robust at origin and appears to be better situated for extending the thigh, while the reverse is the case with the gracilis, which originates farther forward and seems less of an extensor and more of an adductor of the knee than in *Dipodomys*. The biceps mass is relatively more extensive in the jerboas, but it is difficult to see any functional advantage to be derived from the fact that in this group the biceps has split up into several divisions.

Crus. In the three genera dissected there were five sesamoid

bones of the knee in addition to the patella. As usual there was a minute capsular or semilunar sesamoid upon either side, a lateral sesamoid concerned with the gastrocnemius lateralis, a medial one connected with the medial head of this muscle and with the plantaris, and in addition a popliteal sesamoid upon the medial side of the joint, within the tendon of origin of this muscle. There is apparently an increase in the size of the gastrocnemial sesamoids in direct ratio to saltatorial modifications, and they are especially large in *Pedetes*. In an articulated skeleton of the latter all five bones are in place. The gastrocnemial sesamoids are relatively very large indeed, with broad articular surfaces directed toward the articular surface of the condyles, and the lateral one has separate, well marked processes for the attachment of the gastrocnemius and of the plantaris. The popliteal sesamoid also has a broad articular surface.

In all the animals under consideration the crus or shank comprises a single bone, the reduced fibula being firmly fused, at least distally, with the large tibia. The comparative lengths of femur and tibia are especially prone to variation according to specialized habits and this feature is particularly significant in relation to saltatorial ability.

Even the most primitive of mammals are often definitely specialized in some direction and it is somewhat difficult to give instances of what is meant by a generalized type. But it seems probable that in a hypothetical, composite picture of generalized mammals the femur would be a trifle longer than the tibia. That this is actually the case with the wood rat is convenient for purposes of comparison, but after all *Neotoma* is both saltatorial and arboreal to some degree.

If tibia be compared to body length the resulting percentage will be found to be about 30 in *Neotoma*, 52 in *Pedetes*, 57 in *Dipodomys*, 62 in *Scirtopoda*, and 64 in *Allactaga*, indicating an actual, progressive elongation of the crus as leaping ability increases. Expressed in percentage of total limb length (the sum of femur, tibia and pes) it will be found that this value for *Neotoma* is about 33, 35 for *Dipodomys*, again 33 for *Allactaga*, and 30 for *Scirtopoda*. So the relative alteration of this segment is slight and of doubtful import.

The free fibula, or rather the part of it above its fusion with the tibia, is 61 per cent of the tibial length in *Neotoma*, 49 in *Pedetes*, 44 in *Scirtopoda*, and 39 per cent in *Dipodomys* and *Allactaga*. So the tibia-fibular juncture is, in the main, relatively higher in the more saltatorial rodents. In the smaller saltators it could not be demonstrated satisfactorily that the lateral malleolus is composed of the distal fibula (although undoubtedly it is), but in *Pedetes* this was

clearly apparent (as in *Neotoma*) and the element was here attached to the tibia only by connective tissue for a distance of two or more centimeters.

As compared with *Neotoma* the crus is relatively more slender in all of the saltators considered (except *Pedetes*?). *Dipodomys* has the anterior tibial fossa deeper and the posterior shallower, but the proximal part of the fibula and its head are broader, and this anatomical character is largely the case in the jerboas as well, but the posterior fossa is even weaker. As compared with *Dipodomys* the tibia of the jerboas is absolutely more robust, but not relative to length.

In regard to the muscles and mechanics of the thigh the only thing apparent in the present connection is that there is a gradual recession of the hamstring attachments toward the knee accompanying saltation. In other words, in *Neotoma* the semitendinosus or biceps, or both, extend along the shank to a point about 70 per cent the distance from the knee to the heel, while in the saltators this is reduced to less than 50 per cent; indeed but little more than 40 in the case of *Scirtopoda*. It is also apparent that the muscles of the crus proper have shorter muscle bellies and longer tendons in the saltators. This fact is difficult of precise presentation by percentage, but by defining the spot where the muscular part of the gastrocnemii may be said to cease, calling the part of the crus above this spot the muscular part of the shank, and the distance therefrom to the heel as the tendinous part, it will be found in *Dipodomys* that the former comprises 56 per cent of the length of the triceps surae. In *Allactaga* the muscular part is 53, and in *Scirtopoda* 50 per cent of the whole.

Aside from the differences in the muscles of the shank imposed by the digital variation, it is worthy of note that in the jerboas the peroneus longus was very small, doubtless as an accompaniment of the reduction in possible pronation of the joint following saltatorial habits. As suggested by osteological details the tibialis anticus was very robust in *Dipodomys* and *Scirtopoda*, and even larger in *Allactaga*, while the flexor tibialis and tibialis posticus were very weak indeed.

Pes. No rodent is completely digitigrade. All rest with the feet flat upon the ground but as saltatorial ability increases and the foot becomes more springy, an animal will undoubtedly be more prone to stretch upward upon its toes in order to reach above its head to smell or touch some object, than will one not so specialized. And the longer foot will give to it the advantage of being able to stretch farther than the unspecialized sort. But it may be stated as a

generality that during speedy locomotion all rodents fitted for running, as well as leaping, are digitigrade in respect to the pes. That is, when running swiftly the final impulse for projecting the body forward is applied not by the heel, but by the toes not only in the jerboas but in the kangaroo rat, the wood rat, and even in man. Whether the digits themselves are chiefly concerned, however, or merely the distal ends of the metatarsals, is uncertain. For convenience, however, the latter is assumed to be the case, and the effective length of the foot in these animals is therefore presumed to be the distance from the center of the ankle joint to the end of the second longest metatarsal.

In *Neotoma* the pes is but 29 per cent of the body length, while in *Pedetes* this rises to 55, in *Dipodomys* to 58, and in *Allactaga* and *Scirtopoda* to 82 and 95 per cent respectively. So it is seen that when so compared the pes is more than three times longer in this three-toed jerboa than in the wood rat. When the pes is compared with the femur and the tibia the relative positions of the animals are the same. When considered in percentage of total leg length (sum of femur, tibia and pes) it is found that this value is about 32 for *Neotoma*, 37 for *Dipodomys*, 42 for *Allactaga*, and 46 for *Scirtopoda*, showing the greatest relative as well as actual elongation of any of the limb segments accompanying saltatorial specialization.

The chief elements of the tarsus of *Dipodomys* consist of calcaneum, astragalus, navicular, first, second and third tarsales, cuboid, and several sesamoid bones. In comparison with *Neotoma* the tarsus of this genus differs in the following respects:—In the former animal the part of the calcaneum which appears from the lateral aspect to be articulated with the astragalus is somewhat raised. In *Dipodomys* it is sharper and higher, and this may be termed the lateral articular process of the calcaneum. In dorsal view the broad, shelf-like, lateral process of the calcaneum of the wood rat, beneath which pass the peroneal tendons, is much reduced in the kangaroo rat, accompanying presumed reduction in pronation, and it has shifted to the anterior end of the bone. The astragalus has become reduced in length so that anteriorly it does not terminate even with the end of the calcaneum but considerably to the rear, and there is a slight reduction in the size of tarsale 2. The medial tarsal sesamoid, upon which the tibialis posterior inserts, is considerably smaller. In at least some individuals of both kangaroo rat and wood rat there is a minute accessory sesamoid immediately forward of the other, which appears not to be associated with any muscle but rather with the ligamentous structure of the ankle. In *Neotoma* the posterior process of meta-

tarsal 5 is long and falciform, completely covering the peroneus longus canal, but in *Dipodomys* it is much shorter and does not cover the canal. The reduction of this process has probably accompanied a diminution in the importance of the peroneus brevis which inserts thereon, as well as an increase in the tendinous character of the abductor ossis metatarsi quinti. The first metatarsus of *Dipodomys spectabilis* is much reduced but still is considerably longer than any bone in the second or third row of the tarsus.

Ventrally upon the pes of *Dipodomys* the navicular projects in a sharp ridge between tarsale 1 and the calcaneum, which prominence is entirely lacking in *Neotoma*. The sustentaculum tali is much narrower in *Dipodomys*, while the ventral surface of the cuboid is broader. Resting upon (plantarward of) the entoventral process of metatarsus 5 is a small sesamoid from which arise those slips of the flexor digitorum brevis which pass to digits 4 and 5. I have discovered a small sesamoid to occur also in the same position in at least some specimens of *Neotoma*, and the definition of this doubtless increases with age.

In most features, except for a longer cuboid, the tarsus of *Pedetes* resembles that of *Dipodomys*.

In the skeletons of both jerboas before me there is a sesamoid bone, measuring 6.5 mm. in length in *Allactaga*, and 3.5 mm. in *Scirtopoda*, still attached to the heel, its original position having been in the distal part of the calcaneal tendon. In the spirit specimens dissected this part of the tendon had not yet become calcified, but this evidently takes place completely as age advances, and has followed toughening of the tendon. In the jerboas the greater calcaneal process or heel is actually longer (5.7 mm. in *Scirtopoda*, 5.3 in *Allactaga*, and 4.6 in *Dipodomys*), giving greater leverage to the tendon. The lateral articular process of the calcaneum is higher and sharper in both jerboas than in the kangaroo rat, and the trochlear part of the astragalus is more nearly cylindrical (a greater part of a circle). From the dorsal aspect the rest of the tarsus is essentially as in *Dipodomys*, save that in the jerboas the first tarsale is actually longer, with a sharp terminal process plantarward in *Scirtopoda*, with which there articulates the medial tarsometatarsal sesamoid. No muscles are attached to this but against its flattened lateral surface there pass the tendons of the flexores digitorum breves. In *Allactaga*, however, the sesamoid similarly situated, but larger, was located within the original fasciculi of the short flexors to digits 1, 2, and 3.

Upon the lateral side of the foot the abductor ossis metatarsi quinti was reduced in *Dipodomys* and still more so in the jerboas, especially in *Scirtopoda*, in which it was merely a tendinous band. In *Dipodomys* and *Allactaga* it passed from the calcaneum to metatarsus 5 as usual (probably with fibers to the cuboid as well in the latter genus). In *Scirtopoda*, without a fifth toe, it passed to the deeper of the lateral tarsal sesamoids, which appears to be the vestige of a metatarsus 5, and is so termed. In *Dipodomys* the 2 contrahentes appeared to originate from the plantar aspect of the navicular, but there were none in the jerboas.

In *Allactaga* there was a large tarsometatarsal sesamoid at the base of the fifth digit. This was within the original fasciculi of the short flexors to digits 4 and 5, but the true origin of these slips seems to be more precisely from the large plantar process of the cuboid. In *Scirtopoda* this was not the case, and the short flexors of all three digits seemed to take origin directly from this sesamoid, which was located superficially between the cuboid and the vestigial fifth metatarsal. In *Dipodomys* the short flexors appeared to originate as follows: that to digit 2 from the navicular; that to digit 3 from the cuboid; and those to digits 4 and 5 from the lateral sesamoid.

It should be mentioned that as saltation advances and the chief action of the ankle joint is confined more strictly to a single plane, there is a progressive narrowing of the entire tarsus; and that the length of tarsus remains absolutely about the same, except for a slight lengthening of the heel.

The metatarsus of *Dipodomys*, as compared with that of *Neotoma*, is somewhat simpler, the bones are less irregular at base but more crowded together, and in cross section the metatarsal complex is more arched. Otherwise (except for the absence of the fifth) the metatarsi of the two are very similar, not only in detail but in proportions. In *Dipodomys* the percentage of the third when compared to the entire foot length is but two or three points greater than for *Neotoma*. So it is seen that the greater length of foot in *Dipodomys* is gained by elongation both of the metatarsus and digits in practically equal degree. This is particularly well illustrated when the length of metatarsus 3 is compared with the effective leg length. In *Neotoma* this percentage is (in two specimens) between 10 and 11, in *Dipodomys* 18, in *Allactaga* about 28, and in *Scirtopoda* 30, showing that the elongation of this detail progresses at a more rapid rate, as specialization advances, than any other part of the leg.

The step toward saltatorial specialization illustrated by the jerboa

metatarsus as compared with that of the kangaroo rat is a great one. In the jerboas and most of their close allies there is a central "canon bone," formed by the fusion of the second, third and fourth metatarsals. In addition to this there may also be a shorter fifth toe (*Scarturus*), or both a fifth and a first (*Allactaga*, *Euchoreutes*). I do not regard the phylogeny of the foot in these several types of saltators as having been at all uniform, but on the contrary, as involving several processes.

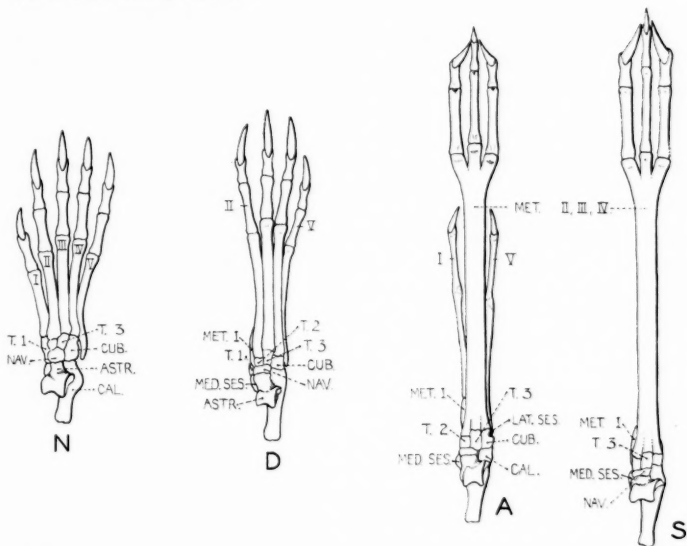


FIGURE 28. Dorsal view ($\times 1$) of the bony details of the pes of *Neotoma* (N), *Dipodomys* (D), *Allactaga* (A), and *Scirtopoda* (S).

The foot of *Scarturus* I regard as being most comparable to that of *Dipodomys*. As in the latter genus it appears likely that the hallux dropped out at an early stage of the more extreme part of its pedal evolution, and that the fifth digit kept relative pace with the others to about the stage now occupied by *Dipodomys*. In the case of the five-toed jerboas the hallux, for some particular reason, was not lost as in *Dipodomys*, but developed at about the same rate as the fifth digit, probably to form a fairly symmetrical pes with five distinct

metatarsals. It seems likely that from this stage (comparable with that of the dipodomysid pes) the saltatorial evolution of the three middle digits of the ancient jerboa stock developed at an augmented pace, rapidly becoming elongated and cemented into a single bone, while the first and fifth toes (where these are now present) ceased further to develop and diminished in importance. Unless these are actually put to some use, such as for scratching (in the case of the hallux) or as an aid in acting as a "snowshoe" in soft sand, these accessory digits are undoubtedly in course of disappearance.

From the above it should not be postulated that *Scirtopoda* and *Dipus* necessarily passed through the same stage as now occupied by *Scarturus* or *Allactaga*. That it may have done so is readily granted, but to me it appears more likely that at the stage comparable to existing *Dipodomys* it had lost both first and fifth digits, as *Salpingotus* has done in advance of the fusion of the three metatarsals.

In *Allactaga* the first phalanges of both first and fifth digits are of about the same length, while the metatarsus of the fifth is somewhat longer than that of the first; but because the first tarsale is so long the claw of the hallux is actually in advance of that of the fifth. In this genus the fifth metatarsal is only 37 per cent of the third, while in *Dipodomys* the former is but a couple of millimeters the shorter.

In the two jerboas under consideration the three main metatarsals are completely fused, save as they tend to split along their original lines of juncture following extreme dessication of the skeleton. The resulting tarsal shaft is even more slender than the distal tibia. Near the base of the toes the bone broadens greatly, and separates into tripartite divisions, each bearing a capitulum for the articulation of a digit. The separation of the three divisions extends a short distance proximal to the end of the bone, undoubtedly for the purpose of affording a surface for the attachment of ligamentous vestiges of the interossei muscles. This point should be noted. The degree of suppression of these ligaments, and of the fusion of the bony surfaces concerned, is a criterion of the specialization for saltation in that it reflects the amount of independent digital movement that is retained.

The metatarsophalangeal sesamoids are slightly smaller in *Dipodomys* than in *Neotoma*, but are much enlarged in the jerboas. It appears certain that the size of these is not determined so much by their acting as anchors for those of the short foot muscles as are attached to them, as it is by their function of pulleys, over which glide the long tendons to the digits.

Except in the matter of length the digits of *Dipodomys* are not

materially different from those of *Neotoma*, save that digit five is relatively shorter in the former. The case of the hallux in the kangaroo rat is of especial interest, however. In certain groups within this genus a rudimentary external hallux is invariably present; and species so characterized were formerly designated generically as *Perodipus*. Other groups invariably lack the hallux, and in still others this feature is present in some individuals and lacking in others; or it may be present upon one foot and absent from the other. As has been pointed out by Grinnell (1922) the reduction of the hallux is least advanced in kangaroo rats of the *ordii* and *microps* groups. "In the *agilis* group, two of the constituent races show occasional individuals in which the claws or phalanges are absent on one or both of the first hind toes. In the *heermanni* group, one race shows occasional lapses, and in two races (*californicus* and *eximius*) the claw and the phalanx which bears it is absent normally, though in one race it is present rarely on one or both hind feet. In the *merriami* and *deserti* groups the process of loss is complete to the extent that only a rudiment of the first metatarsal is present." The latter is not the condition in *D. spectabilis*.

In *Dipodomys*, as in the jerboas, the conformation of the phalanges of digits 2 and 4 is such that the tips, and hence the nails, are slightly inclined toward digit 3, as indicated not only by the position of the digits but by the facts that their nails are a bit more worn upon the side adjoining digit 3. This clearly suggests that there is a slight tendency in the kangaroo rat, more accentuated in the jerboas, for the animal to group the three central digits as closely as possible.

In the two sorts of jerboas under consideration the bones, and even the nails, of digits 2 and 4 are more robust than of 3. The first phalanx of the third is also slightly longer than of the other two digits, and this is apparently accentuated by the greater slenderness of this digit and by the fact that its metatarsophalangeal joint is situated farther forward. The terminal phalanx of the third digit is also extended so that its axis is at a right angle with the axis of the second phalanx. This condition has apparently been brought about by hypertension of the tendon of the extensor digitorum longus to this digit, and relaxation of the tone of this branch of the flexor tibialis. This tendency, but in much reduced form, is exhibited by digits 2 and 4 also, especially in *Allactaga*. The result is that the unusually globular, terminal pads of the digits are applied to the ground in a triangular pattern, and the nails are well elevated.

As it may be considered that all the short muscles of the jerboa

foot have either disappeared or become tendinous there is possible no independent movement of the toes. In other words such movement of the toes in relation to the metatarsus as may take place is involuntary, as far as the foot is concerned, and is governed involuntarily by extension and flexion of the entire pes through the musculature of the crus. It is unlikely that this would result in any definite abduction of the toes. On the contrary the tendency appears to be for adduction of the digits and a grouping of the digital pads into a single complex. Concomitant to this is a clear trend toward the twisting of the second and fourth digits so that their nails incline toward that of the third, precisely as in *Dipodomys* save to a more pronounced extent. Undoubtedly this feature is correlated with a tendency toward grouping of the three digits, or in other words a tendency for the three to function largely after the fashion of a single, more robust digit.

Conclusions.

On the whole, the characters which fit a rodent for a saltatorial existence are seldom of a sort which can be placed in a table, as present or absent. Mostly they comprise slight differences in proportion, increase in the length of the pes, reduction in size of the lateral digits, and so forth. But rarely can there be listed such a definite item as fusion of the metatarsals. It seems clear that specialization for a saltatorial existence involves alteration of the physiological mechanism of nerve impulse and muscle reaction to fully as definite a degree as it does change in gross bodily form, and the former cannot be evaluated.

Speaking in general terms the impression is given by a study of the anatomy of the rodents dissected in the present instance that saltatorial specialization affects both the heteromyid and dipodid stocks in the following particulars:

There is some degree of broadening of the face, and a progressive weakening of the masticatory musculature, but the first of these details at least is only secondarily attributable to saltation, because of bullae enlargement.

There is experienced an increase in size of the auditory apparatus, with enlargement of the mastoid chiefly, and of the tympanic part of the ear to a lesser extent. If such enlargement be but moderate the external ear may also be very large. If increase in size of the mastoid features be of phenomenal degree, then the external ear will be either small or of medium size.

There is an increase in the shortness of the neck, already short in rodents.

There appears to be a shortening of the trunk with increased saltation, although this is difficult of proper determination.

There is an apparent increase in the strength, and in the complexity, of the long back musculature, associated with its use in connection with the hind limbs in leaping.

There is a decrease in the robustness of the arm, possibly with a slight relative shortening of this member, and the latter character is accentuated in appearance by the increase in length of the hind limb.

There is experienced a progressive increase in the postacetabular length of the innominate as compared with the preacetabular measurement, as well as a relative shortening of the presacral part of the ilium.

There is a progressive elongation of the hind limb, especially distally. Thus the relative elongation of the pes is greatest, of the shank less, and of the thigh least of these three segments: or, expressed in another way, if the sum of the thigh, shank and foot length be taken as 100, then it will be found that with saltatory specialization there will be progressive shortening of the thigh, and elongation of the foot, while the length of the shank in relation to total limb length experiences a very slight reduction.

There is, probably, a slight reduction in the importance of the fibula as compared with more generalized rodents, but this is not pronounced.

There is a phenomenal increase in the length of the pes, involving both metatarsus and digits. The breadth of the pes decreases and there is compaction of the bony elements, this, in the most specialized sorts, resulting in fusion of the central metatarsi. There is usually a tendency toward reduction and eventual elimination of the side digits (with accompanying change of tarsal details) but the final disappearance of these may be long delayed. The muscles of the foot proper will become tendinous.

The perissodactyl or odd-toed type of pes is eventually attained, save that in the most highly specialized sorts the third digit is more slender than the second and fourth. The two latter digits have their nails inclined toward the third, so that there is a tendency for the grouping of the digits into a functional unit. The result of these hind limb specializations is the assumption of a bipedal, saltatorial, digitigrade gait. There is no discernible indication that these rodents

will eventually become monodactyl, or that when resting they will ever cease to be plantigrade.

In anatomical details the most specialized of the jerboas are apparently far in advance of the kangaroo rats in saltatorial features. Whether the former also surpass greatly in saltatorial performance remains to be determined.

It is interesting to note that the most generalized of the Heteromyidae are not discernibly fitted for leaping; hence, that within this family saltatorial specialization varies from very poor to very good. In the Dipodidae, on the other hand, although one member (*Sicista*) of a nearly related family is generalized, saltatorial specialization, on the whole, varies from good to astonishingly good. In other words dipodids are considerably better fitted for leaping than are heteromyids. The facts are suggestive of the thesis that, providing other factors were equal, North America has not maintained an arid, "desert" type of plains country where this now occurs for as long, or at least as uninterrupted, as has the Old World. Or, stated differently, the Dipodidae have evidently been exposed to saltatorial influences for a longer period of time than the Heteromyidae.

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